## *An investigation into the impact of environmental change upon the vegetation of Widdybank fell, upper Teesdale*

Lewthwaite, Katherine Jane

# An investigation into the impact of environmental change upon the vegetation of Widdybank Fell, Upper Teesdale

by

Katherine Jane Lewthwaite

*Department of Biological Sciences,*

*University of Durham.*

*1999.*



Submitted in partial fulfilment of the requirements for the degree of

Doctor of Philosophy

*"And the waters prevailed, and were increased greatly upon the earth." (Genesis 17:18)*

**Frontispiece: Widdybank Fell and Cow Green Reservoir.**

## Declaration

The material contained within this thesis has not previously been submitted for a degree at the University of Durham or at any other University. The research reported within this thesis has been conducted by the author unless indicated otherwise.

## Abstract


- Widdybank Fell is located in the Upper Teesdale National Nature Reserve in the Northern Pennines. It is internationally renowned for its unique late-glacial relict assemblage of plant species, particularly those on the "sugar limestone" outcrops. Cow Green Reservoir was constructed in the early 1970s and flooded the lower western slopes of Widdybank Fell. At the time there was concern amongst ecologists that the reservoir might alter the local climate and have adverse effects on the remaining vegetation.

- A comprehensive vegetation survey of Widdybank Fell was carried out by Jones (1973). Aspects of this survey were repeated as part of the present study. There have been significant changes in the composition of some of the plant communities since the 1970s. These changes include a considerable loss of bryophyte diversity and lichen abundance. Overall there has been a decline in "stress tolerant" species, and a loss of calcicole species on the calcareous grasslands. Few of the nationally rare plant species have changed in abundance.

- Using data from the meteorological stations at Widdybank Fell and from nearby Moor House, it has been demonstrated that the presence of Cow Green Reservoir has resulted in significant changes in the local climate. These changes are consistent with those expected by a classic "lake effect" and include the all year round moderation of minima (e.g. resulting in a reduction in the number of ground frosts). The reservoir has also produced cooler mean air temperatures in spring and warmer mean temperatures in autumn.

- Despite the observed local climate impact of Cow Green Reservoir it seems most likely that other factors have been responsible for the observed vegetation changes. Acid deposition has probably caused the loss of calcicoles on the calcareous grasslands, and atmospheric nitrogen deposition could explain the loss of bryophyte diversity and lichen abundance.

## Acknowledgements

I would like to thank my supervisors, Dr Bob Baxter and Professor Brian Huntley for their consistent support and enthusiasm throughout my project. I would also like to thank my colleagues in the Environmental Research Centre, particularly Dr Judy Allen, for their help and advice. Thanks are also due to Mr Eric Henderson for construction of the microcosm frames and point quadrat and for putting up with some less-than-ideal fieldwork conditions! Dr Margaret Bradshaw and Mrs Margaret Pullen both proved invaluable sources of botanical knowledge.

Thanks are also due to a number of institutions and people who provided me with meterological data: Mr John Adamson, Ms Mandy Lane and Dr Terry Parr at the Environmental Change Network (Institute of Terrestrial Ecology, Merlewood), The British Atmospheric Data Centre, Mr Ian Findlay and Mr Andy Joyce. Mr Steven Willis kindly allowed me to make use of the vegetation data from his unpublished MSc thesis. The Photographic Unit at the Department of Biological Sciences, University of Durham provided the photographs used in Plates 2.1-2.6 & 7.1 and Dr John Daniell the photographs in Plates 7.3 and 7.4. The photographs comprising the frontispiece were provided by NERC.

I would like to thank the past and present English Nature wardens of Widdybank Fell, Mr Ian Findlay and Mr Chris McCarty for their great help to me over the duration of this project. Thanks are also due to the Raby Estate for allowing me access to the Fell and to Dr Chris Spray at Northumbrian Water for the provision of the automatic weather station.

This studentship was funded for two years by the Teesdale Trust and for the remaining year by the University of Durham.

Finally I must thank my parents for their love, encouragement and support. This thesis is dedicated to the memory of my grandmother Maud Lewthwaite (1913-1997).

# Contents

## List of Tables

# List of Figures

**Appendix D**

## List of Plates

## Maps and overlays (in thesis pocket)

### Maps

1:10000 scale map of the vegetation of Widdybank Fell

1:25000 scale maps of the vegetation of Widdybank Fell:

Sheet 1 (Slapestone Sike)

Sheet 2 (Sand Sike)

Sheet 3 (Red Sike

Sheet 4 (Fold Sike)

Sheet 5 (Tinkler's Sike)

### Overlays

Overlay to 1:10000 scale map

Overlay to Sheet 1

Overlay to Sheet 2

Overlay to Sheet 3 (a)

Overlay to Sheet 3 (b)

Overlay to Sheet 4

Overlay to Sheet 5

## Notes on nomenclature used in this thesis

Vascular plants follow Clapham, Tutin and Moore (1987)

Mosses follow Smith (1980)

Liverworts follow Smith (1990)

Lichens follow Purvis *et al.* (1992)

# 1. Introduction

## *1.1 General background*

Upper Teesdale is located on the eastern slopes of the Northern Pennines of England (Figure 1.1). The Upper Teesdale National Nature Reserve lies at 300 to 700 m above sea level and includes Widdybank (G. R. NY820290) and Cronkley Fells (G. R. NY840270).

The flora of Upper Teesdale has long been of interest to naturalists. John Binks, a lead miner, was reputedly responsible for the discovery of many of the so called "Teesdale rarities" in the late 1700's, for example *Gentiana verna* (Smith & Sowerby, 1798). *Minuartia stricta* was first recorded by Backhouse (1844) and Widdybank Fell is still the only recorded locality in Britain for this species (Clapham, 1978). Some of the plant communities that are particularly unusual in Upper Teesdale are associated with the unique saccharoidal or "sugar" limestone outcrops on Widdybank and Cronkley Fells. Rarities found in such communities include *Viola rupestris* and *Kobresia simpliciuscula.*

The Teesdale flora is considered to be a late-glacial "relict" assemblage derived from a previously more geographically widespread vegetation type. Many of the species found in Teesdale today have disjunct modern distributions. For example, *Alopecurus alpinus* has an Arctic circumpolar distribution and Teesdale is its most southerly European locality (Elkington, 1978). In contrast, *Helianthemum canum* has a Mediterranean distribution and Teesdale is its most northerly European locality (Meusel & Jager, 1992). These "relict" species have managed to persist despite periods of extensive forest development. The presence of a wide range of open habitat niches such as cliff ledges, marshes and flushes may have acted as refugia for species intolerant of closed canopy vegetation (Pigott & Walters, 1954).

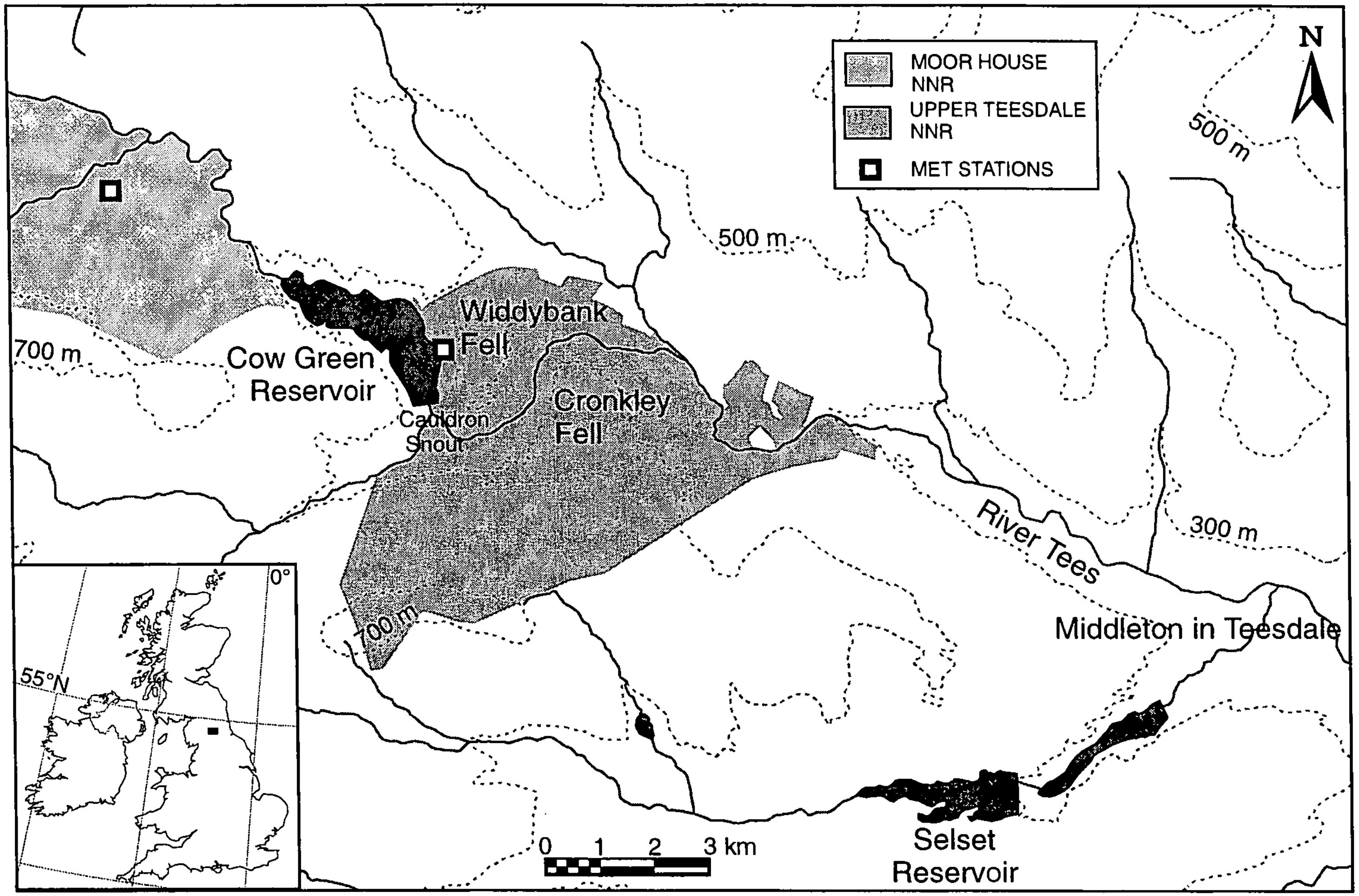



**Figure 1.1 Location map of Upper Teesdale.**

The continued existence of these species today is thought to be a result of the combination of a cool, wet climate, a continued history of grazing (mainly by sheep) and the low soil nutrient status, especially on the sugar limestone (Jeffrey & Pigott, 1973).

### 1.2 Cow Green Reservoir

In 1965 it was proposed by the Tees Valley and Cleveland Water Board that a dam should be built across the Tees valley at Cauldron Snout. This was in order to provide a water storage reservoir, for use principally by industrial plants of the Imperial Chemical Industries Limited on Teesside. The proposal was strongly opposed by ecologists (Lousley, 1965; Gregory, 1975). An area of vegetation covering 3.1 x $10^6$ $m^2$ would be flooded, of which 0.1 x $10^6$ $m^2$ was at that time designated as a Site of Special Scientific Interest (S.S.S.I.). This region, on the lower western slopes of Widdybank Fell, contained grasslands on the sugar limestone outcrops (Gregory, 1975).

As well as this direct destruction by flooding, concern was also raised as to the possible consequences of reservoir construction upon the remaining vegetation. It was proposed that changes in the local climate could occur as a result of the presence of a large body of water (Bellamy, 1965; Bradshaw, 1966). This was considered to be a real threat to some of the rare species, especially those at the edges of their geographic ranges. Such species would be expected to be especially sensitive to climate change (Lousley, 1965; Bradshaw, 1966; Godwin & Walters, 1967) although the effects might be different for species at the northern and southern limits of their ranges.

Despite these concerns, Parliament ruled that the need for the water was urgent and no other sites on the Tees were feasible for construction of a reservoir. Only a small area of the S.S.S.I. designated grasslands would be destroyed and "steps could be taken to protect the remainder". Hence in March 1967 the "Tees Valley and Cleveland Water Bill" became law (Nugent, 1978) and the completed reservoir first began to fill in the autumn of 1971.

### 1.3 Vegetation surveys

At the time of reservoir construction an extensive phytosociological survey of Widdybank Fell was carried out by Jones (1973). The major plant communities (ombrogenous bog, heath, marsh and acid and calcareous grasslands) were classified using Zurich-Montpellier phytosociology. The classes were subdivided into 31 mapping units or "noda" and vegetation maps were produced to locate the positions of each nodum on the fell.

There have been two recent vegetation surveys of Widdybank Fell. Willis (1995) re-examined six of the vegetation noda defined by Jones (1973) which represented each of the major plant communities on the fell. These were:

- Festuco-Brometea, calcareous grasslands, Nodum with *Calluna vulgaris* (Nodum 4)
- Molinio-Arrhenatheretea, calcareous grasslands, Nodum with *Carex caryophyllea* (Nodum 21)
- Oxycocco-Sphagnetea, wet heath, Nodum with *Erica* and *Trichophorum* (Nodum 23)
- Sphagnetalia magellanici, dry heath, Nodum with *Narthecium* and *Trichophorum* (Nodum 24)
- Nardo-Callunetea, acid grassland, Nodum with *Galium saxatile* and *Sphagnum papillosum* (Nodum 29)
- Calluno-Ulicetalia, acid grassland, Nodum with *Danthonia decumbens* (Nodum 33)

Each nodum was located using the vegetation maps of Jones (1973) and surveyed using quadrats and the Domin scale of cover-abundance. The most striking changes between the two vegetation surveys had occurred Nodum 33. In this nodum, 34 new species were present (i.e. species not recorded in Jones' survey) including *Achillea millefolium* and *Thymus praecox* subsp. *arcticus*. Changes were also observed in the limestone heath, Nodum 4; most noticeably the newly recorded *Agrostis vinealis.* In Nodum 21 a number of new species were recorded, for example *Ditrichum flexicaule*.

Another recent survey (Maxwell, 1997) also investigated Nodum 4 (the limestone heath community). Sampling was carried out along a transect on the south western slope of the fell to investigate any present-day differences in species abundance with distance from the reservoir. A linear point quadrat was used to sample at intervals along the transect, starting at the reservoir edge and up to a distance of 900m from the reservoir. Three species showed statistically significant differences with distance from the reservoir: *Festuca ovina* (more abundant by the reservoir) and *Sesleria albicans* and *Dicranum scoparium* (less abundant by the reservoir).

### 1.4 The aims and outline of this thesis

The aim of this thesis is to establish whether there have been significant changes in the vegetation of Widdybank Fell since the construction of Cow Green Reservoir. Any such changes are then interpreted with reference to environmental factors that may have altered over this period. In addition to the predicted modification of the local climate by the reservoir, other factors that are considered include changes in grazing pressure, changes in regional climate and changes in the deposition of atmospheric pollutants. A brief outline of the thesis is given below:

**Chapter 2**

This chapter contains a detailed background to the study on Widdybank Fell including its climate, geology and past and present vegetation.

**Chapter 3**

The null hypothesis that (notwithstanding earlier work) there has been no change in the vegetation of Widdybank Fell since the survey of Jones (1973) is tested by repeating aspects of her vegetation survey.

**Chapter 4**

This chapter examines the ecological and physiological traits of species that have changed in abundance between the vegetation survey of Jones (1973) and the present day survey.

**Chapter 5**

The null hypothesis that Cow Green Reservoir has had no effect on the local climate is tested using records from the meteorological station on Widdybank Fell and records from nearby Moor House.

**Chapter 6**

This chapter presents an examination of other environmental and management factors that may have changed in the period between the two vegetation surveys.

**Chapter 7**

The null hypothesis that the vegetation of Widdybank Fell is insensitive to temperature change is tested using a microcosm experiment on two grassland types along an altitudinal transect.

**Chapter 8**

Chapter 8 is a general discussion of the results of this study, and considers the implications and wider relevance of the work.

### 1.5 Summary

- Upper Teesdale is located in the Northern Pennines and Widdybank Fell, the area covered by this study, lies within the Upper Teesdale National Nature Reserve. The flora of Upper Teesdale has been of long and continued interest to naturalists, particularly the unique assemblage of species on the sugar limestone soils. Many of these species are relicts from the late-glacial period.

- The proposal to construct a reservoir that would flood floristically rich areas of Widdybank Fell was met with strong opposition by ecologists. As well as the loss of the area flooded, there was concern that the reservoir might produce changes in the local climate that could threaten the remaining rare species. Despite these concerns, construction of the reservoir was authorised and the area was flooded in 1971.

- A comprehensive vegetation survey of Widdybank Fell was carried out by Jones (1973). Recent surveys have indicated that there have been changes in some of the plant communities on the fell. The major aim of this thesis is to further investigate what changes may have occurred and to suggest likely causes.

# 2. Background to the study

## *2.1 Upper Teesdale in context with similar areas*

Two of the best known features of Upper Teesdale are the presence of an unusual substrate (the sugar limestone) and the collection of phytogeographically disjunct species. Distinctive underlying geology is often responsible for the unusual nature of the associated vegetation and may be responsible for apparent disjunctions in species distributions. This can be seen, perhaps most commonly, in calcicole vegetation on soil over calcareous outcrops. Geochemical anomalies often produce even more specialist floras, as few plant species can tolerate the physically unfavourable or toxic conditions. Serpentine rocks, for example, where calcium is replaced by magnesium as the dominant cation, tend to result in soils which are nutrient poor, often prone to drought and may be rich in metals such as nickel, chromium and cobalt (Jeffrey, 1987). Such soils have particular plant communities that can tolerate the physically and chemically unfavourable conditions, such as the Violetea calaminariae which is adapted to cope with the metals present at toxic levels (Birse, 1982). The plant communities on such soils are often of low stature and open-structured. Distinctive morphological or chromosomal races of species can also arise under such conditions, for example the hexaploid *Campanula rotundifolia* found on the serpentine Lizard peninsula on the Cornish coast (Ratcliffe, 1977).

There are a number of areas that bear some floristic similarity to Upper Teesdale. The Baltic island of Öland off the southern Swedish coast is renowned for its open "alvar" grassland, found on thin, poorly-drained soils over a flat limestone plain. Like Upper Teesdale the Öland flora includes phytogeographically disjunct species, some of which are at the margins of their range. Species found in common with Teesdale include *Primula farinosa, Polygala amarella, Antennaria dioica, Linum catharticum* and *Draba incana* (Ekstam *et al.* 1984).

Within the British Isles there are also regions similar to Upper Teesdale. These include the Breckland of East Anglia, Ben Lawers in the Eastern Highlands of Scotland, the Craven district of the Pennines in North Yorkshire and the Burren in County Clare, Western Ireland. All these areas have species with disjunct distributions, some of which are in common with Teesdale, but none of the areas have identical floras to Teesdale.

The Breckland is a lowland chalk outcrop with a complex mosaic of different soil types (depending on the nature and depth of the deposits over the chalk). The Breckland's calcareous heath grasslands are particularly species-rich: *Carex ericetorum* and *Rhytidium rugosum* are two rarities found that also occur in Upper Teesdale (Trist, 1979). Ben Lawers, reaching an altitude of 1214 m, has a base-rich mica-schist substrate with a rich Arctic-Alpine flora; species such as *Dryas octopetala*, *Saxifraga aizoides*, *Draba incana*, *Thalictrum alpinum* and *Carex capillaris* are in common with Teesdale (Ratcliffe, 1977). The Craven Pennines is an upland area of Carboniferous limestone. It has a number of important limestone features (karst) with dry valleys, disappearing streams and underground caves and extensive areas of limestone pavement. It has some montane plant species such as *Dryas octopetala*, *Draba incana* and *Minuartia verna* which it shares in common with Teesdale (Ratcliffe, 1977).

The Burren, in Western Ireland, is a lowland area of Carboniferous limestone, also renowned for its karst scenery and it shares several rare species with Upper Teesdale including *Dryas octopetala*, *Helianthemun canum* and most notably *Gentiana verna*. Similar to Teesdale, the Burren has a remarkably disjunct modern flora. Not only are Arctic-Alpine species present, but more recent additions are species with southern distributions that take advantage of the currently warmer climate, such as the orchid *Neotinea intacta* which is of Mediterranean range (Ivimey-Cook & Proctor, 1966). All these sites that have been described share some similar habitats niches to Teesdale such as cliff ledges, marshes and flushes which, similar to Teesdale may have acted as unforested refugia for late-glacial species to survive to the present. All these localities hence play an important role in interpreting the evolution of the modern flora of the Northern Hemisphere (Bradshaw, 1965).

## 2.2 Topography of the study area

Widdybank Fell has a flat summit at 526.5 m O. D. covering around 1.8 $km^2$ (Bradshaw & Jones, 1976) and steep scarps on the south and east sides overlooking the River Tees (See 1:10000 map in thesis pocket). The fell is drained on all sides by small streams (sikes). The lower western slopes of the fell were flooded in 1971 following the construction of the dam on the River Tees at Cow Green. The reservoir covers an area of 3.12 $km^2$ with a maximum depth of 22.9 m (Tees Valley and Cleveland Water Board *pers. comm.*).

## 2.3 Climate

The three factors important for determining the climate of a region are latitude, relief and proximity to the sea (Pigott, 1978a). Upper Teesdale, at latitude 54° 40 'N, is almost equidistant from the Irish Sea and the North Sea and within 80 km of both. The climate data given below are from the Widdybank Fell manual meteorological station (513 m O. D.) Records are taken from the period January 1968 to November 1995.

Winter temperatures are low and are not greatly ameliorated by the influence of the sea because of the effects of altitude. February, the coldest month, has a mean daily minimum air temperature of -2.2 °C and grass minimum of -3.3 °C with a mean of 0.1 °C (Figure 2.1). Ground frosts can occur in any month and the average number of days with snow lying each year is 63. Summers are very cool due to a synergistic effect of sea and altitude. Summer temperatures, at their peak in July, reach a mean monthly maximum of 16.1 °C, with a monthly mean of 12.3 °C. Widdybank Fell is often wet and windy. Average wind speed in the calmest month is 6.2 $m\ s^{-1}$ and the mean annual rainfall is 1560 mm, with precipitation on 250 days a year.

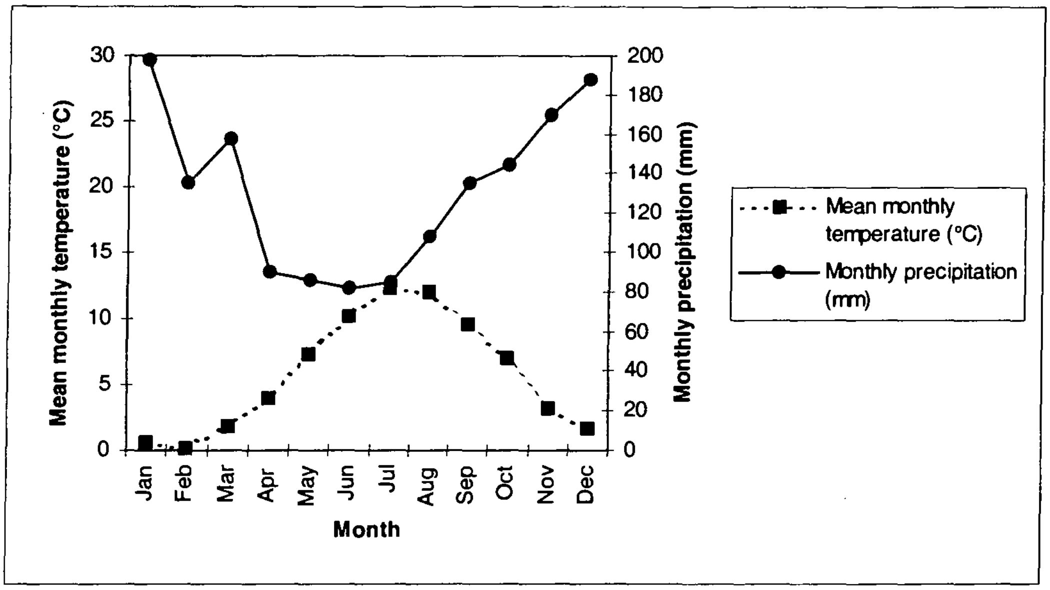



**Figure 2.1 Climate diagram for Widdybank Fell *sensu* Walter (1979) showing mean monthly temperature and monthly precipitation over the period 1968 to November 1995. Relative scaling of axes is modified from that of Walter (where conventionally 10 °C is equivalent to 20 mm of precipitation) such that 15 °C is equivalent to 100 mm of precipitation.**

These climatic characteristics mean that this part of Upper Teesdale has been described as "sub-Arctic", although the summers are generally cooler, wetter and more cloudy than true sub-Arctic tundra (Coulson, 1978; Walter, 1979).

## *2.4 Geology and soils*

### *2.4.1 Bedrock*

Most of the rocks in Upper Teesdale were laid down during the Carboniferous period and belong to the Lower and Upper Limestone Series (the exceptions are the slates and ash of the Lower Palaeozoic-Ordovician). The carboniferous limestone beds are of various thicknesses and are interbedded with shales and sandstones. The quartz-dolerite Great Whin Sill was intruded into this sequence at the end of the Carboniferous. The Whin Sill is exposed as steep jointed faces and cliffs along the Tees valley, most notably at High Force (Pigott, 1956). The intrusion of the Whin Sill into the sedimentary rock resulted in localised metamorphosis. Pure Melmerby Scar limestone became coarsely crystalline marble. When exposed and weathered this marble breaks down into separate calcite crystals and is known as saccharoidal or "sugar" limestone. Although found in other areas of Teesdale, the sugar limestone only forms outcrops of significant size on Widdybank and Cronkley Fells (Valentine, 1976). The outcrops of weathered rock bear some resemblance to calcareous dunes (Plate 2.1).

On Widdybank Fell the bedrock is dominated by Melmerby Scar limestone, with a small outcrop of Robinson limestone in the north west. These are both of the Lower Limestone Group and are particularly associated with the rare plants of Teesdale (Johnson, Robinson & Hornung, 1971). Falcon Clints on the south side of Widdybank Fell overlooking the Tees is a Whin Sill outcrop, and there are other outcrops on the eastern edge of the fell. On Widdybank Fell there is also an exposed bank of sugar limestone, which due to its south-westerly aspect, is exposed to strong winds and rain and hence is subject to erosion. The water-permeable sugar limestone lies over impermeable dolerite or metamorphosed mudstone. Consequently, small springs or "sikes" emerge along the edge of these outcrops (Figure 2.2). The springs tend to undercut the sugar limestone and cause more erosion. The calcareous water flows out over the impermeable surface to form extensive areas of wet gravel, known as "flushes".

### *2.4.2 Soil types*

All soils in Upper Teesdale post-date the last Weichselian (Devensian) glaciation. The types of soil that have developed in this area depend on the depth and nature of the deposits over the bedrock and the water regime (Pigott, 1978b). The most widespread soils in Upper Teesdale are the so called "hydromorphic soils" that are formed as a result of impeded drainage (either due to topography or the impervious substrate beneath). Such soils have an anaerobic component and generally low pH and vary from shallow, wet mineral soils (derived from parent rock) to deep peat (Pigott, 1978b). The sugar limestone outcrops (where not eroded bare) are associated with varying depths of glacial drift (Figure 2.2).

**Plate 2.1 Sugar limestone outcrop on Widdybank Fell.**


**Plate 2.2 Typical Nodum 1 vegetation. Note the large proportion of bare ground and the cushion of *Minuartia verna* (arrowed).**

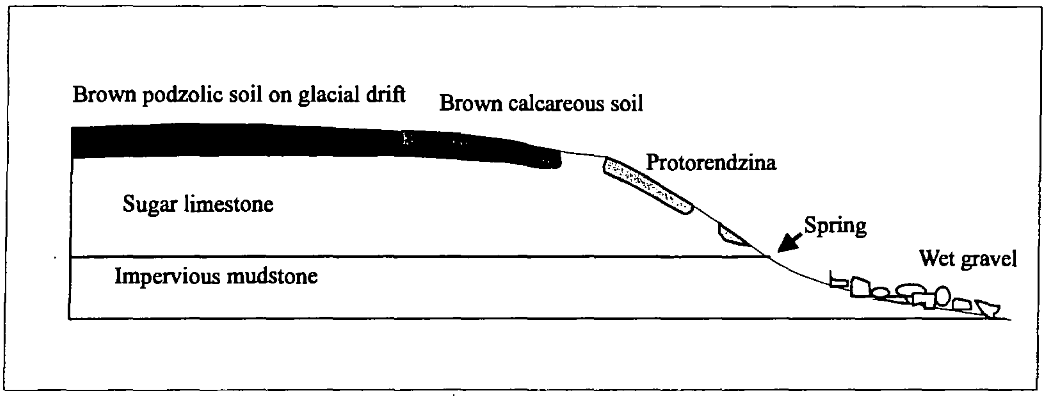



**Figure 2.2 Cross section through a sugar limestone outcrop to show different soil types (from Pigott, 1978b).**

In the deepest areas of drift, peaty gley or organic soils occur. Shallower areas of drift tend to be associated with brown calcareous soils. These are in many ways similar to brown earths developed on unaltered limestone. Soil pH is usually around 7.0 but may be lower in the upper part of the soil profile. In areas where the limestone is covered by only a thin layer of glacial drifts, mull rendzinas or shallow brown calcareous soils arise. Typical pH values range from 7.0-8.0. Despite the high rainfall, the thin rendzinas and brown earths on the sugar limestone outcrops dry out rapidly and very high moisture tensions occur in most summers. This restricts successful colonisation and growth to species with xerophytic adaptations (Welch & Rawes, 1972).

The mosaic of different vegetation types seen on Widdybank Fell is thus largely a consequence of the heterogeneous soil types present. The particular vegetation associated with the different soil types is described in Section 2.7. The thesis of Jones (1973) includes chemical analyses and profiles of the soils associated with each vegetation nodum. The low standing crop and productivity in many grassland areas (Bellamy *et al.*, 1969) which persists even with cessation of grazing, is often a result of the low soil nutrient status. Fertilisation experiments on a sugar limestone outcrop on Widdybank Fell dominated by *Festuca ovina* and *Sesleria albicans* and a flushed region dominated by *Kobresia simpliciuscula* demonstrated that available phosphate was the major factor limiting plant growth (Jeffrey & Pigott, 1973). This low availability of phosphate may be due to the fact that the sugar limestone soils are lead-rich; the lead may be preventing successful plant uptake (Jeffrey, 1971).

### 2.5 Land use

Probably the most profound impact of man's activity in Upper Teesdale has been tree clearance. There is evidence in the pollen record from Red Sike Moss on Widdybank Fell of a sudden change from woodland dominated by *Quercus* and *Alnus* species to grassland and blanket bog around 2600 BP (Turner *et al.*, 1973). Following this initial clearance, grazing on the fells by sheep, cattle and horses prevented tree regeneration. Modern day grazing is still an important influence on the vegetation. Flocks of Swaledale sheep graze the upper dale in summer, but are moved down to the enclosed fields near the farm, known as "inby" land, in winter. Sheep tend to graze the limestone grasslands in preference to the areas of heath or bog (Willis, 1995). However, grazing on the grass heath may prevent individual *Calluna* bushes from forming a closed canopy and thus maintain the grassland patches.

The short and sparse nature of the turf in many areas of Widdybank Fell is not however primarily a result of grazing, as exclosure experiments have demonstrated. Sheep exclusion for 20 months on a flushed area of the fell dominated by *Kobresia simpliciuscula* (Jeffrey & Pigott, 1973) resulted in little vegetation change. Exclusion over the same period on sugar limestone turf dominated by *Festuca ovina* and *Sesleria albicans* also produced little change apart from some increase in cover in *Sesleria.* In a longer-term experiment Elkington (1981) found that a 12 year exclosure of sheep and rabbits on sugar limestone on Cronkley Fell produced relatively few changes in species cover and abundance. He noted an increased frequency of the dwarf shrubs *Dryas octopetala* and *Helianthemum canum.* Only *Gentianella amarella* was lost as a result of cessation of grazing. Maintenance of the species-rich communities on the sugar limestone appears therefore, to be predominantly due to the limitation of available soil phosphate. Biomass removal through grazing and the cool climate will also aid the depression of plant production and allow the survival of species that are intolerant of shade or aggressive competition.

Areas of heath on Widdybank Fell are managed for red grouse (*Lagopus scoticus*) but they are "only moderately suitable for this purpose" according to Roberts (1978). Hence they may have escaped the persistent burning regime that is generally used to maintain stands of heather of mixed ages. The grouse feed on the newly regenerated areas and use the older stands for shelter.

In addition to the formation of the sugar limestone, intrusion of the Whin Sill into the sedimentary limestones resulted in the formation of veins rich in barytes and galena, which have been mined for the last two centuries (Jones, 1973). Lead veins are often found near the surface of the ground and channels from open cast lead mining are a common feature of the dale. These channels and their associated spoil heaps are still visible in many areas (including Rod's Vein on Widdybank G. R. NY814303) as a result of limited colonisation by plants. Heavy metal tolerant species are found growing in these areas. Vegetation of the Violetea calaminariae is an example on Widdybank.

Tourism is an important part of the economy of Upper Teesdale. Around the time of reservoir construction it was estimated that Widdybank Fell received fifty thousand visitors annually although today the figure is still high at around forty thousand (C. McCarty, *pers. comm.).* Trampling pressure in the vicinity of the Birkdale track (the footpath across the fell) can be intense.

Roberts (1978) sums up the human impact on Upper Teesdale as "sustained but light interference" and of insufficient intensity to remove the Arctic-Alpine rarities as a result of the remoteness and inaccessibility of the area.

## *2.6 Vegetation history and phytogeographical affinities of the flora*

### *2.6.1 Vegetation history*

As described in Chapter 1, the Teesdale flora is considered to contain a component of late-glacial "relict" species that previously occupied a more widespread geographic range. Blackburn (1931) and others have suggested that the relict species must have survived in ice free patches during the last glacial period. Current evidence however indicates that such ice free areas were unlikely; glacial depth is believed to have been 1700 m above sea level in the Teesdale region (Boulton, 1977). Godwin (1949) proposed instead that the plants reached Upper Teesdale as colonisers following the retreat of the ice ten to fifteen thousand years ago. Analysis of pollen and macrofossils (Turner *et al.*, 1973) from peat cores at Widdybank Fell demonstrated that the species present during the late-glacial (11-15000 BP) at this site were similar to those found in other areas of Britain. However, unlike in other areas, these late-glacial species persist in the pollen record throughout the post-glacial at Widdybank.

Certain habitat niches were probably important as refugia for the relict species. These refugia included: areas above the tree line, inland cliffs and screes, river banks, marshes and flushes, and shallow soils over limestone (Pigott & Walters, 1954). *Gentiana verna*, for example, probably survived around calcareous sikes during the forest period and later was able to extend its range (Turner, 1978). On Widdybank and Cronkley Fells the unstable, eroding nature of the sugar limestone outcrops may have been of particular importance in creating a series of open habitats during the forest period (Johnson *et al.*, 1971).

The isolation of the Teesdale rarities from other populations for around nine thousand years has resulted in subtle variation in some species. These differences may be morphological; for example the difference in compactness of growth form in *Viola rupestris* between Teesdale and nearby Cumbrian sites (Valentine & Harvey, 1961). Some chromosomal variation can occur and although Teesdale populations are usually similar to those in the rest of Britain there are exceptions, for example the chromosome number of *Alopecurus alpinus,* where 2n=100 in

Teesdale but 2n=117 in the rest of Britain (Fearn, 1971). Elkington (1978) gives a comprehensive list of chromosomal and morphological variation in the Teesdale flora. Clearly these distinct races of phytogeographically disjunct species in Teesdale are a valuable resource for research.

### *2.6.2 Phytogeographical affinities of the flora*

Various methods have been used for classifying the biogeography of the British vascular flora. One of the most recent, Preston & Hill (1997) subdivides the flora into nine major biome categories, based on their occurrence in one or more major biomes (e.g. Arctic) and their longitudinal distribution. Each of these nine categories is represented by species in the Teesdale flora (Table 2.1).

The Widdybank flora is of phytogeographical interest because many of the species have disjunct distributions. For example, *Gentiana verna* (European Arctic-montane floristic element) is found in Teesdale and Cumbria. *Thalictrum alpinum* (Circumpolar Arctic-montane floristic element) covers the mountains, whereas *Minuartia stricta* (in the same element) is confined to flushes on Widdybank Fell in Britain (Elkington, 1978). *Helianthemum canum* (Mediterranean montane) is confined to western Britain and has Teesdale as its most northern British locality. *Polygala amarella* (European Boreo-temperate) and *Carex ericetorum* (Eurosiberian Boreo-temperate) have similar distributions and are both found in north and south-east England. Species distributions are taken from Meusel and Jager (1992).

Many factors are responsible for determining species distributions. One believed to be of importance for certain montane species is maximum summer temperature (Dahl, 1951). Although such species are generally restricted to regions of high altitude in central Europe, the increased latitude in Britain enables their survival at lower altitudes. *Gentiana verna* is found mainly between 1000-2500 m in the Alps, but as low as 400 m in Teesdale and at sea level in the Burren in Co. Clare, Ireland (Pigott, 1978a). As a result of factors such as sensitivity to maximum summer temperature, species at the edges of their

**Table 2.1 Biogeography of the Widdybank flora. Species from Jones (1973); floristic elements from Preston & Hill (1997).**

| Major biome category (identifying number in brackets) | European Distribution of species within each major biome category | Numbers of species in the Widdybank flora in each major biome category | Floristic elements represented in the Widdybank flora (identifying number in brackets) | Examples |
|---|---|---|---|---|
| Arctic-montane (10) | Species with their main distribution north of or above (on mountains) the tree line | 8 | European Arctic-montane (13)<br>Circumpolar Arctic-montane (16) | *Gentiana verna*<br>*Minuartia stricta* |
| Boreo-arctic Montane (20) | Species occurring in the Arctic-montane and Boreal montane zones | 24 | European Boreo-arctic montane (23)<br>Eurosiberian Boreo-arctic montane (24)<br>Circumpolar Boreo-arctic montane (26) | *Draba incana*<br>*Potentilla crantzii*<br>*Carex capillaris* |
| Wide-boreal (30) | Species distibution centred on the Boreal zone but also found in the Arctic and Temperate zones | 16 | Eurosiberian Wide-boreal (34)<br>Eurasian Wide-boreal (35)<br>Circumpolar Wide-boreal (36) | *Plantago maritima*<br>*Ranunculus acris*<br>*Cardamine pratensis* |
| Boreal-montane (40) | Species distribution centred on the Boreal zonobiome or in coniferous forest in southern mountains | 20 | Suboceanic Boreal-montane (42)<br>European Boreal-montane (43)<br>Eurosiberian Boreal-montane (44)<br>Eurasian Boreal-montane (45)<br>Circumpolar Boreal-montane (46) | *Galium sterneri*<br>*Viola lutea*<br>*Vaccinium myrtillus*<br>*Primula farinosa*<br>*Pinguicula vulgaris* |
| Boreo-temperate (50) | Species found equally in the Boreal and Temperate zones (if absent from the Boreal zonobiome found in the subalpine region on mountains) | 97 | European Boreo-temperate (53)<br>Eurosiberian Boreo-temperate (54)<br>Eurasian Boreo-temperate (55)<br>Circumpolar Boreo-temperate (56) | *Polygala amarella*<br>*Carex ericetorum*<br>*Achillea millefolium*<br>*Gentianella amarella* |
| Wide-temperate (60) | Species distribution is centered on the Temperate zone but also in the Boreal and Southern zones | 11 | Eurosiberian Wide-temperate (64)<br>Circumpolar Wide-temperate (66) | *Anthoxanthum odoratum*<br>*Agrostis stolonifera* |
| Temperate (70) | Species have their main distribution in cool- temperate, broad leaved deciduous forest zone | 63 | Oceanic temperate (71)<br>Suboceanic temperate (72)<br>European temperate (73)<br>Eurosiberian temperate (74)<br>Eurasian temperate (75)<br>Circumpolar temperate (76) | *Erica cinerea*<br>*Polygala serpyllifolia*<br>*Briza media*<br>*Carex caryophyllea*<br>*Viola rupestris*<br>*Koeleria macrantha* |
| Southern temperate (80) | Species found equally in the Southern and Temperate zones | 12 | European Southern-temperate (83)<br>Eurosiberian Southern-temperate (84)<br>Eurasian Southern-temperate (85) | *Carex flacca*<br>*Plantago lanceolata*<br>*Lotus corniculatus* |
| Mediterranean (Southern) (90) | Species with their main distribution in the warm-temperate zone south of the broad-leaved deciduous forest zone | 3 | Mediterranean-montane (93) | *Helianthemum canum* |

geographic ranges (as is the case for certain elements of the Teesdale flora) may be especially sensitive to climate change.

### *2.7 Plant communities of Widdybank Fell*

The major plant communities found on Widdybank Fell are ombrogenous bog, heath, marsh and calcareous grassland. The blanket bogs and wet heaths dominated by *Calluna vulgaris* and *Sphagnum* species are the most widespread vegetation type on the fell and are common to many upland areas. Surrounding these are other areas of heath or rough grassland. Few of the rare plants of Upper Teesdale are associated with the plant communities on these acid peat or peaty gley soils (Pigott, 1978b).

Calcareous grasslands have developed both on unaltered and sugar limestone. The dry grasslands upon the two different limestones share many species in common, for example *Festuca ovina*, *Sesleria albicans*, *Campanula rotundifolia*, *Thymus praecox* subsp. *arcticus* and rarities including *Gentiana verna*. The similarity in these grasslands is not surprising considering that the brown calcareous soils that have developed on parts of the sugar limestone have been shown by analysis to be similar to those on the unaltered limestone (Pigott, 1978b). However certain plant species are associated particularly with the shallow rendzina soils over the sugar limestone outcrops. These include *Polygala amarella*, *Viola rupestris*, and *Carex ericetorum* with *Kobresia simpliciuscula* and *Primula farinosa* occurring in flushed or marshy areas (Ratcliffe, 1978).

Areas of limestone heath occur on Widdybank Fell where there is a moderate depth of glacial drift over the sugar limestone. These areas are transitional between the grasslands on the shallow drift and the acid heath on the deep drift and contain a mixture of species from both communities; those associated with limestone grassland, including *Festuca ovina*, *Sesleria albicans* and *Campanula rotundifolia* and heath species, predominantly *Calluna vulgaris* (Ratcliffe, 1978). Leaching of the upper layers of the soil profile is probably responsible for the co-existence of calcicole and calcifuge species, the *Calluna* rooting in the upper, leached layer and the calcicoles with the majority of their roots in the lower base-rich layers. Such a phenomenon is described by Gimingham (1960).

Jones (1973) used Zurich-Montpellier phytosociology to classify the vegetation of Widdybank Fell. Such a technique is described by Shimwell (1971). The Widdybank Fell vegetation was ultimately divided into 31 mapping units or "noda" (a term first adopted by Poore, 1955). A set of five vegetation maps of selected areas of the fell was produced at a scale of 1:25000 (Sheets 1-5 in thesis pocket) and a smaller scale map of the vegetation of the whole fell at 1:10000 (in thesis pocket). The key found on each map shows the vegetation classification in detail.

The study described in this thesis focused on nine noda, the seven noda on the sugar limestone soils (Noda 1-7) a nodum on unaltered limestone (Nodum 21) and one on acid grassland (Nodum 33). The reasons for selection of these noda are discussed in Chapter 3. Field keys to these nine noda based on Jones (1973) are given in tables (i)-(iii) in Appendix A. These illustrate the division of each association into its respective noda, based on differential species.

**Class Festuco-Brometea, calcareous grasslands (Association Seslerio-Caricetum pulicaris Shim. 1969 emend.)**

Seven noda were recorded in this association at Widdybank, (Noda 1-7, see vegetation map Sheet 3, for example areas) and all were used in the present investigation. These noda best correspond to the modern National Vegetation Classification (NVC) (Rodwell, 1992b) as the CG9d sub-community i.e. Calcicolous grasslands: *Sesleria albicans-Galium sterneri* grassland, *Carex capillaris-Kobresia simpliciuscula* sub-community. (Classification by Willis, (1995) using computer program MATCH (Malloch, 1992)). The CG9d sub-community is confined in Britain to sugar limestone in Upper Teesdale i.e. it is only found on Widdybank and Cronkley Fells and has no apparent European counterpart (Rodwell, 1992b).

**Nodum 1: Nodum with *Kobresia simpliciuscula*** syn.: *Kobresia* sub-var

**Nodum 2: Nodum with *Rhytidium rugosum*** syn.: *Rhytidium* sub-var

These noda are both found on the eroding sugar limestone outcrops, where up to 40 % of the area can be unvegetated, and in the closed turf above and below these outcrops. Presence or absence of *Kobresia simpliciuscula* is used to distinguish the two noda in the field as *Rhytidium rugosum* is only locally abundant. There is a high cover of *Sesleria albicans* forming a coarse turf. Other species with high cover-abundance (i.e. dominants) include *Carex ericetorum*, *Thymus praecox* subsp. *arcticus* and *Helianthemum nummularium*, with *Minuartia verna* being locally abundant. A typical area of such vegetation (classified as Nodum 1) is shown in Plate 2.2.

**Nodum 3: Nodum typicum of γ Nodal group with *Minuartia verna***

syn.: sub-ass. typicum typical var. p.p.

Similar to Noda 1 and 2, Nodum 3 comprises a coarse turf (not illustrated). However it is not generally found adjacent to the sugar limestone outcrops. The turf is composed of *Carex capillaris*, *C. flacca* and *C. panicea*, with *Minuartia verna* locally abundant.

**Nodum 4: Nodum with *Calluna vulgaris* syn.:** sub-ass. typicum *Calluna-Empetrum* var.

This nodum includes the areas of limestone heath as described above. *Calluna vulgaris* is the dominant species (Plate 2.3).

**Nodum 5: Nodum with *Plantago lanceolata*** syn.: sub-ass. typicum typical var. p.p.

The differential species for this nodum are *Plantago lanceolata*, *Hieracium pilosella* and *Thuidium tamariscinum*. Also found are species particularly associated with grazing and manuring such as *Bellis perennis* and *Trifolium repens*. On areas of limestone "pavement" on the fell plateau (e.g. vegetation map Sheet 1, G. R 817302) a hummock-hollow vegetation complex forms. On first inspection the vegetation appears similar, but the hummocks are classified as

**Plate 2.3 Nodum 4 vegetation. Note the mixture of *Calluna vulgaris* and grass species.**

**Plate 2.4 Nodum 7 vegetation. Note the presence of *Kobresia* (in brown autumn colour) and a rosette of *Primula farinosa* (arrowed); a differential species for this nodum.**

Nodum 5 and the hollows Nodum 21. (Nodum 5 is not illustrated, but see Plate 2.5 of Nodum 21). Additionally, Noda 4 and 5 are often found adjacent to each other and were sometimes mapped together by Jones (1973) where they formed a mosaic pattern.

**Nodum 6: Nodum typicum of γ Nodal group with *Kobresia simpliciuscula***
syn.: *Kobresia* var. -typical sub-var.

The turf is generally dominated by *Kobresia simpliciuscula* along with *Sesleria albicans*, *Festuca ovina* and *Carex capillaris.* It is often found adjacent to the eroding sugar limestone. Nodum 6 is not illustrated here, but bears close resemblance to Nodum 7 (Plate 2.4).

**Nodum 7: Nodum with *Primula farinosa*** syn.: *Kobresia* var. *Carex lepidocarpa* sub-var

The differential species for this nodum are *Primula farinosa, Carex lepidocarpa* and *C. hostiana.* Dominant species include *Kobresia simpliciuscula, Sesleria albicans*, *Festuca ovina* and *Carex capillaris.* This nodum is found in moist, usually strongly calcareous, regions such as on banks next to the sikes (streams) draining the fell. Plate 2.4 shows a typical area of Nodum 7 vegetation.

**Class Molinio-Arrhenatheretea, calcareous grasslands**

**(Association Festuco-Nardetum ass. nov. prov.)**

Four noda were recorded in this association at Widdybank; Noda 19, 20, 21 and 22, of which only Nodum 21 is described. Vegetation map Sheet 1, G. R. NY815302 shows an area of Nodum 21 vegetation. In terms of NVC classification (Rodwell, 1992b), Nodum 21 best matched CG10 (*Festuca ovina-Agrostis capillaris-Thymus praecox* grassland, specifically CG10a, the *Trifolium-Luzula* sub-community) and also matched CG9 (*Sesleria albicans-Galium sterneri* grassland), but did not fit entirely into either group (Willis, 1995). CG10a is found in association with calcareous rocks and soil in scattered localities across the British uplands. CG9 communities are more confined in distribution, found on the Carboniferous limestone of Northern England (Rodwell, 1992b).

**Nodum 21: Nodum with *Carex caryophyllea***

This nodum forms a relatively fine-leaved and usually closed turf with differential species including *Danthonia decumbens*, *Carex caryophyllea*, *Campanula rotundifolia*, *Viola lutea*, *Achillea millefolium*, *Koeleria macrantha*, *Alchemilla glabra* and *Carex pilulifera*. There are also scattered patches of *Sesleria albicans* and *Nardus stricta*. The nodum is found in various types of habitat ranging from the steep slopes above the sikes on the fell, to the grassland by the Birkdale track (vegetation map Sheet 1; G. R. NY815302) and the hollows of a hummock-hollow complex. A typical area of Nodum 21 grassland is illustrated in Plate 2.5.

**Order Calluno-Ulicetalia (in the Class Nardo-Callunetea), acid grasslands (Vaccinium myrtillus heath-Calluna vulgaris complex Bridgewater 1970 p.p.)**

Four noda were recorded for this association, Noda 26, 31, 32 and 33 of which the latter only is described. In terms of NVC classification the match was poor, with Nodum 33 most similar to H18 (*Vaccinium myrtillus-Deschampsia flexuosa* heath) (Willis, 1995) which occurs widely across the British uplands, especially in northern Scotland (Rodwell, 1992a).

**Nodum 33: Nodum with *Danthonia decumbens***

Nodum 33 comprises dry, relatively species-poor turf composed of *Agrostis* and *Festuca* species, *Cladonia arbuscula* and *C. uncialis* with *Galium saxatile* and occasional *Vaccinium myrtillus*. *Danthonia decumbens* and *Carex caryophyllea* are the two differential species. Unlike in the other noda in the association, *Calluna vulgaris* is virtually absent. A typical area of Nodum 33 is illustrated in Plate 2.6. This nodum sometimes forms distinctive hummock/hollow complexes, for example on the Birkdale track at the road entrance to Widdybank Fell (Vegetation map Sheet 1, G. R. NY815305).

**Plate 2.5 Nodum 21 vegetation with *Alchemilla glabra* (arrowed) the most clearly visible differential species.**

**Plate 2.6 Nodum 33 vegetation. Notice the relatively fine-leaved sward.**

## 2.8 Summary

- To set the study in Upper Teesdale in context, a number of other areas in the British Isles with distinctive substrate types or floras containing phytogeographically disjunct species are described.

- Widdybank Fell covers an area of c. 1.8 $km^2$ at an altitude of c. 520 m O. D. It has a cold, wet and windy climate, with the potential for ground frosts all the year round. Carboniferous limestones form the majority of the bedrock of the fell. In some areas, intrusion of the Whin Sill has lead to the formation of saccharoidal or "sugar" limestone. The free-draining rendzinas and brown earths on the sugar limestone outcrops are prone to drought and are low in available phosphate, both factors that potentially limit plant colonisation.

- Historically, man's major impact in Upper Teesdale has been through tree clearance. This was followed by the introduction of grazing (predominantly by sheep) which prevented tree regeneration. On the sugar limestone grasslands however, exclosure and fertilisation experiments have demonstrated that phosphate limitation rather than grazing is the primary factor that maintains a short sward.

- The flora contains late-glacial relict species that previously occupied more widespread geographic ranges. Many of these species have disjunct phytogeographical distributions. Where species are at the northern or southern limits of their geographic ranges they may be most sensitive to climate change.

- Jones (1973) classified and mapped the vegetation of Widdybank Fell. A selection of the mapped plant communities are described: the communities on the sugar limestone (Noda 1-7 in the class Festuco-Brometea), a community on unaltered limestone (Nodum 21 in the class Molinio-Arrhenatheretea) and an acid grassland community (Nodum 33 in the class Calluno-Ulicetalia).

# 3. Vegetation survey

## 3.1 Introduction

The work described in this chapter was designed to test the null hypothesis that there has been no significant change in the vegetation of Widdybank Fell since 1969, notwithstanding the limited evidence for change from recent surveys (Willis, 1995; Maxwell, 1997). The comprehensive vegetation survey of Widdybank Fell carried out by Jones (1973) between 1967 and 1969 was used as the baseline for comparison with a present-day survey.

## 3.2 Methods

### 3.2.1 *Survey methods*

It would have been possible to repeat the entire Widdybank vegetation survey of Jones (1973) classifying the resulting relevés using Zurich-Montpellier phytosociology. This would have been excessively time-consuming to the exclusion of other proposed investigations in the project. Instead it was deemed more appropriate in the context of the hypothesis posed, to concentrate the survey within a selection of previously defined and mapped noda (similar to the survey of Willis 1995). As already described in Chapter 2 these were Noda 1-7, 21 and 33; which were selected for the following reasons:

Noda 4, 21 and 33 were included in the survey of Willis (1995) since they cover the largest area of their class. In each of these three noda, some changes in species composition and relative abundance had been noted (see Chapter 1).

Noda 1-3 and 5-7, all classified in the Festuco-Brometea, were also selected. These noda included the plant communities on the sugar limestone that are unique to Upper Teesdale. Consequently, these communities are of international importance and of high conservation value and any change noted would be of interest. Many of these communities are open-structured, with high proportions of bare ground and eroding substrate, hence there may be greater potential for gap invasion and change in community composition than in the closed turf grasslands. Noda 1-7 are also widespread on the fell, covering more than a third of the total area mapped by Jones (1973).

The quadrats used by Jones in her survey were unfortunately not marked *in situ.* Hence the survey of Willis (1995) had been based on a "pseudorandom" selection of nodal patches. Since then however, sketch maps and aerial photographs of the fell showing some of Jones' quadrat positions have been found to survive. These quadrat positions for the nine noda under study were transferred onto the respective 1:25000 vegetation maps of the fell (see Sheets 1-5 and their overlays in thesis pocket) which were then used in the field. Fortunately, these maps still delimit accurate boundaries between noda (Willis, 1995).

Even though quadrats could generally be placed in the field with some degree of accuracy (within an estimated 2 m of the original in all except the largest nodal patches) the surveyor was ultimately required to make a decision as to final quadrat position. As a result, care was taken to avoid boundaries between noda and to select a "typical" area of the stand in terms of its species composition and relative abundance, as would have been done in the original survey.

Nodum identity was confirmed in each quadrat using the keys to noda from Jones (1973), reproduced in Appendix A. Quadrats were marked in the field by means of wooden posts; quadrat size corresponded to that used in the original survey, which ranged from 0.25 to 4.0 square metres. All species occurring in the quadrat were listed and assigned a cover-abundance rating using the Domin scale. The version of this scale used was the same as in the survey of Jones, which was somewhat unconventional, so is reproduced in Appendix B.

### *3.2.2 Additional quadrats*

Inevitably, not all the sketch map positions of quadrats used by Jones could be used in the present survey, for one of three reasons:

- Their position was not recorded on any surviving sketch map.
- Their position lay in the area now flooded by Cow Green Reservoir.
- There was a poor correspondence between Jones' sketch map and Jones' colour vegetation map.

The number of relevés used by Jones for the initial classification of noda also varied considerably. Where the number originally collected was small or their positions could not be used in the present survey, additional quadrats were surveyed where necessary, so a minimum of ten relevés were obtained in the present survey for each nodum. Quadrat size was the same as had been used most frequently by Jones for each nodum. This size was confirmed as suitable following assessment using species-area curves. These serve to estimate the minimal quadrat area required to provide a representative sample of the vegetation to be recorded (Kershaw & Looney, 1985).

The additional quadrats were located in order to complement the positions of the quadrats already surveyed. The present survey thus provided good coverage of nodal patches right across the fell, including areas closest to, and furthest from, the reservoir margin. These additional quadrats are also marked on the overlays to the vegetation maps (Sheets 1-5) and numbered starting at 800 (Numbers 1-560 used by Jones, numbers 501-737 were used by Willis (1995) for his survey). Table (i) in Appendix B includes a list of all quadrats in each nodum that were used in the original and present surveys.

Field surveying was carried out in the summers of 1996 and 1997. Quadrats were generally surveyed in early summer and rechecked later in the season to avoid bias if some species were especially conspicuous or inconspicuous at certain times.

### *3.2.3 Data analysis*

In order to test the null hypothesis that there has been no change in the vegetation of Widdybank Fell since 1970, the relevés from the original survey of Jones were compared with those from the present survey for each of the nine noda under study. Most of the relevés collected in the survey of Jones for each nodum were used for data analysis (irrespective of whether or not their positions had been used in the present survey). The exceptions to this are detailed in Appendix B and Appendix B Table (i). As described earlier, relevés from the present survey comprised those positioned based on quadrats in the original survey and the additional quadrats, recorded where the former were scarce.

The primary investigation tested for any difference in the overall composition of the vegetation for each nodum between surveys. Hence relevés from the present and original surveys were compared for each separate nodum using Canonical Correspondence analysis (CANOCO) (TerBraak, 1988). The relevés from the present and original surveys for each nodum were combined and the "environmental variable" on which the first canonical axis was based was the source of the data, either present or original. The significance of this axis was tested using a Monte Carlo permutation test (TerBraak, 1988).

Additionally, for each species recorded, the frequency of occurrence among all relevés in the nodum, in both the present and original surveys, was calculated. Median Domin score was also calculated for each species in each survey as a measure of abundance. Any change in species frequency or abundance between the two surveys was then classified using the criteria in Table 3.1. The significance of these changes was assessed by comparing the (raw) Domin scores for each species between the two surveys using a Mann-Whitney U-test, suitable for such non-parametric data.

**Table 3.1 Criteria for assessing changes in individual species frequency or abundance between the original (Jones, 1973) and present surveys.**

| Name | Abbreviation (used in results tables) | Criteria |
|---|---|---|
| New | N | The species was not recorded in the original survey in any relevés of the nodum under study, but now occurred in at least one relevé in the present survey. |
| Absent | A | The species was recorded in at least one relevé for the nodum in the original survey but was not now found in any relevés of the nodum in the present survey. |
| increased | + | The median Domin score for the species in the present survey had increased compared to the original survey and/or the frequency of occurrence of the species had increased by at least 0.2. |
| decreased | - | The median Domin score for the species had decreased in the present survey compared to the original survey and/or the frequency of occurrence of the species had decreased by at least 0.2. |
| unclear change | +/- or -/+ | Frequency and abundance had changed according to the criteria above but in opposite directions. The first symbol refers to frequency of occurrence of the species, the second after / refers to its abundance. |
| unchanged | u | Neither frequency or abundance have changed between the two surveys according to the criteria stated above. |

## *3.3 Results*

There was a significant difference ($P \leq 0.05$) in overall vegetation composition between the two surveys for five of the nine noda under study: Noda 2, 4, 5, 7 and 33 (Table 3.2, below). Total numbers of species recorded between surveys had increased in Noda 1, 2, 3 and 33 and decreased in Noda 4, 5, 6, 7 and 21. However individual species that had changed significantly between surveys had most often decreased in abundance since the survey of Jones (1973). Table (ii) in Appendix B gives the frequency and Domin scores for all species in all noda. Table 3.3 lists the individual species that had significantly changed (in frequency or abundance, according to the criteria above) in at least one nodum. Table (iii) in Appendix B lists the remainder of the species. (Note: the raw data from the vegetation survey is archived on CD at the University of Durham).

**Table 3.2 Results from the CANOCO Monte Carlo simulation for each nodum and from Mann-Whitney U-tests carried out on individual species in each nodum.**

| Nodum | Total number of species recorded in the survey of Jones (1973) | Total number of species recorded in the present survey | P value in CANOCO Monte Carlo simulation | Number of species that had significantly changed in frequency or abundance between the two surveys (refer to criteria above) in the Mann-Whitney U-test | | | |
|---|---|---|---|---|---|---|---|
| | | | | new | increased | decreased | absent |
| 1 | 43 | 54 | 0.076 | | 1 | 4 | 1 |
| 2 | 45 | 52 | 0.016 | | 1 | 3 | 2 |
| 3 | 56 | 68 | 0.127 | | 1 | 6 | 1 |
| 4 | 95 | 63 | 0.005 | 2 | 3 | 10 | 4 |
| 5 | 111 | 87 | 0.005 | | 2 | 13 | 3 |
| 6 | 73 | 57 | 0.314 | | | 8 | 2 |
| 7 | 96 | 66 | 0.045 | | | 11 | 1 |
| 21 | 101 | 82 | 0.298 | | | 3 | |
| 33 | 59 | 72 | 0.002 | 1 | 1 | 4 | 3 |

The main species that had changed significantly within each nodum are summarised below. For all noda except 21, more species had changed in abundance than would be expected by chance alone when performing multiple Mann-Whitney tests.

### Nodum 1: Nodum with *Kobresia simpliciuscula*

Despite the fact that the CANOCO Monte Carlo simulation was not significant for this nodum (i.e. there was no overall change in vegetation composition between the two surveys), six individual species had significantly changed in frequency or abundance. There were no species newly recorded in sufficient

**Table 3.3 Results from Mann-Whitney U-tests comparing raw Domin data between the present and original surveys for each species recorded. U values and significance levels (* where $P \le 0.05$, ** where $P \le 0.01$) are given. Changes in species frequency or abundance are indicated as new (N) i.e. the species was only recorded in the present survey; absent (A) i.e. the species was only recorded in the original survey; increased or decreased in frequency (+ or - respectively) or changing differently in terms of its frequency and abundance (+/- or -/+ respectively). See Table 3.1 for more detailed explanation of symbols.**

**Summary information used for Mann-Whitney U-tests**

| | NODUM 1 | NODUM 2 | NODUM 3 | NODUM 4 | NODUM 5 | NODUM 6 | NODUM 7 | NODUM 21 | NODUM 33 |
|---|---|---|---|---|---|---|---|---|---|
| Number of quadrats (previous survey, present survey) | 7,11 | 8,10 | 5,10 | 12,12 | 19,16 | 13,13 | 12, 10 | 8,11 | 7,10 |
| Critical values for U with number of quadrats as above | $p \le 0.05$ =61<br>$p \le 0.01$ =67 | $p \le 0.05$ =63<br>$p \le 0.01$ =69 | $p \le 0.05$ =42<br>$p \le 0.01$ =46 | $p \le 0.05$ =107<br>$p \le 0.01$ =117 | $p \le 0.05$ =212<br>$p \le 0.01$ =230 | $p \le 0.05$ =124<br>$p \le 0.01$ =135 | $p \le 0.05$ =91<br>$p \le 0.01$ =99 | $p \le 0.05$ =69<br>$p \le 0.01$ =75 | $p \le 0.05$ =56<br>$p \le 0.01$ =61 |

**Species for which there was a significant difference in frequency or abundance between surveys in at least one nodum**

**Forbs and shrubs**

| | NODUM 1 | | NODUM 2 | | NODUM 3 | | NODUM 4 | | NODUM 5 | | NODUM 6 | | NODUM 7 | | NODUM 21 | | NODUM 33 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change |
| *Anemone nemorosa* | | | | | | | 108.0* | N | 153.0 | - | | | | | | | | |
| *Calluna vulgaris* | 42.0 | N | | | 26.0 | + | 125.0** | + | 180.5 | N | 91.0 | A | 68.0 | + | 52.0 | N | 41.5 | - |
| *Campanula rotundifolia* | 42.5 | - | 47.0 | + | 33.5 | - | 119.0** | - | 246.5** | - | 113.5 | N | 86.0 | - | 67.0 | - | 47.0 | - |
| *Euphrasia rostkoviana* | 68.0** | - | 41.0 | u | 47.5** | - | 105.0 | - | 275.5** | - | 163.0** | - | 89.5 | - | 73.5* | - | 49.0 | N |
| *Galium sterneri* | 39.0 | - | 48.0 | + | 38.0 | - | 125.0** | - | 202.5 | - | 121.0 | u | 68.5 | u | 65.5 | - | 42.0 | N |
| *Gentianella amarella* | 55.0 | + | 56.0 | + | 44.5* | + | 72.0 | u | 181.5 | + | 118.5 | + | 88.0 | + | 60.0 | + | 42.0 | N |
| *Hieracium pilosella* | | | 45.0 | A | 30.5 | + | 78.0 | A | 224.5* | + | 90.5 | A | 65.0 | | 50.5 | +/- | 38.5 | u |
| *Linum catharcticum* | 41.0 | u | 53.5 | - | 40.0 | - | 76.0 | - | 259.5** | - | 114.0 | - | 68.0 | - | 54.0 | + | 42.0 | N |
| *Potentilla erecta* | 41.0 | + | 44.0 | N | 35.5 | - | 115.5* | - | 217.5* | - | 111.5 | - | 94.0* | - | 51.0 | - | 53.0 | - |
| *Selaginella selaginoides* | 45.5 | -/+ | 45.0 | A | 44.0* | - | 110.0* | - | 254.0** | - | 130.0* | - | 103.0** | - | 65.0 | - | 42.0 | N |

**Table 3.3 continued**

| | NODUM 1 | | NODUM 2 | | NODUM 3 | | NODUM 4 | | NODUM 5 | | NODUM 6 | | NODUM 7 | | NODUM 21 | | NODUM 33 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change |
| *Thymus praecox* subsp. *arcticus* | 69.5** | - | 70.0** | - | 45.5* | - | 91.5 | u | 299.0** | - | 162.0** | - | 108.0** | - | 83.0** | - | 63.0** | N |
| *Viola lutea* | 42.0 | N | 44.0 | N | 27.0 | + | 86.5 | + | 231.0** | + | | | 74.0 | + | 46.5 | + | 54.0 | +/- |
| *Viola rupestris* | 61.5* | - | 59.5 | - | 28.0 | - | | | 153.5 | u | 90.0 | - | 61.5 | - | 48.0 | N | | |

## Grasses, sedges and rushes

| | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Agrostis capillaris* | 42.0 | N | | | 27.5 | N | 124.0** | + | 272.5** | + | 91.0 | N | 64.0 | + | 56.0 | + | 43.0 | - |
| *Agrostis stolonifera* | | | | | 27.5 | N | 108.0* | A | | | 91.0 | A | 63.5 | + | 49.5 | -/+ | 44.5 | -/+ |
| *Agrostis vinealis* | | | | | | | 108.0* | N | | | | | | | | | 45.0 | A |
| *Anthoxanthum odoratum* | | | | | | | 120.5** | + | 154.0 | + | | | | | 45.0 | u | 55.0 | + |
| *Briza media* | 44.0 | - | 41.0 | + | 30.5 | - | 117.0* | - | 196.0 | - | 109.0 | - | 73.0 | u | 54.0 | - | 49.5 | - |
| *Carex capillaris* | 42.0 | N | 44.0 | N | 37.5 | - | 72.5 | + | 196.0 | - | 140.5** | - | 91.5* | - | 52.0 | N | 42.0 | N |
| *Carex caryophyllea* | | | 44.0 | N | 39.5 | -/+ | 104.0 | - | 154.0 | u | 110.5 | A | 64.0 | + | 70.0* | - | 37.5 | u |
| *Carex hostiana* | | | | | | | 84.0 | A | | | | | 95.0* | A | | | 40.0 | A |
| *Carex panicea* | 67.0* | + | 48.0 | N | 27.0 | u | 115.0* | - | 157.5 | u | 91.0 | u | 65.5 | + | 59.0 | + | 37.0 | u |
| *Carex pilulifera* | | | | | | | | | | | | | | | 66.0 | A | 60* | A |
| *Carex pulicaris* | | | | | | | 120.5** | - | 220.5* | - | 117.0 | A | 85.0 | A | 62.0 | - | 42.0 | N |
| *Danthonia decumbens* | 50.5 | -/+ | 50.5 | N | 25.5 | A | 91.0 | - | 244.5** | - | 122.5 | A | 65.5 | -/+ | 61.0 | -/+ | 65.5** | - |
| *Festuca ovina* | 54.5 | + | 63.5* | + | 31.5 | u | 85.5 | u | 178.5 | + | 89.0 | + | 79.0 | + | 51.5 | + | 46.0 | - |
| *Koeleria macrantha* | 57.5 | -/+ | 63.0 | - | 35.0 | - | 86.5 | -/+ | 178.0 | | 146.5** | - | 67.0 | -/+ | 45.5 | +/- | 42.0 | + |
| *Sesleria albicans* | 51.0 | - | 45.5 | -/+ | 26.0 | + | 97.0 | - | 238.5** | - | 85.0 | + | 83.5 | - | 45.5 | + | | |

## Mosses

| | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Ctenidium molluscum* | 59.5 | - | 50.0 | - | 32.0 | - | | | 195.0 | - | 132.0* | - | 105.0** | - | 49.0 | +/- | | |
| *Dicranum scoparium* | | | | | 27.5 | N | 76.5 | - | 227.5* | + | 96.0 | - | 66.0 | N | 62.5 | - | 67.0** | - |

**Table 3.3 continued**

| | NODUM 1 | | NODUM 2 | | NODUM 3 | | NODUM 4 | | NODUM 5 | | NODUM 6 | | NODUM 7 | | NODUM 21 | | NODUM 33 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change |
| *Ditrichum flexicaule* | 66.0* | A | 69.5** | - | 40.0 | - | 78.0 | A | 191.0 | - | 123.5 | - | 108.0** | - | 48.0 | N | | |
| *Fissidens adianthoides* | 43.0 | + | 43.0 | - | 29.0 | - | 72.0 | u | 206.0 | - | 113.5 | - | 109.0** | - | 51.5 | - | | |
| *Hylocomium splendens* | 42.0 | N | 43.5 | + | 32.0 | -/+ | 73.5 | N | 196.5 | - | 90.5 | + | 68.5 | - | 57.5 | - | 57.5* | +/- |
| *Hypnum cupressiforme* var. *lacunosum* | 43.5 | - | 49.0 | -/+ | 30.0 | - | 110.0* | - | 166.0 | - | 99.5 | - | 96.0* | - | 47.0 | - | 42.0 | N |
| *Hypnum jutlandicum* | | | | | | | 77.0 | +/- | 209.0 | - | 92.0 | - | 72.0 | N | 53.0 | + | 69.0** | - |
| *Pleurozium schreberi* | | | | | 30.0 | - | 94.5 | - | 208.0 | A | | | | | 55.5 | - | 62.0** | - |
| *Racomitrium canescens* | 52.0 | - | 70.0** | A | 43.0* | - | 78.0 | A | 181.0 | u | 113.5 | - | 70.5 | - | 54.5 | - | 36.5 | u |
| *Racomitrium lanuginosum* | 42.5 | - | 42.0 | - | 50.0** | - | 114.0* | - | 211.0 | - | 105.5 | - | 79.0 | u | 48.5 | - | 41.5 | + |
| *Rhytidiadelphus loreus* | | | 45.0 | A | | | 120.0** | A | 176.0 | A | | | | | | | | |
| *Tortella tortuosa* | 59.0 | - | 62.5 | - | 37.5 | - | 79.0 | - | 175.0 | u | 122.5 | - | 93.0* | - | 56.0 | N | | |

**Liverworts**

| | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Frullania tamarisci* | 44.0 | A | 45.0 | A | 35.0 | A | 90.0 | A | 216.0* | - | 117.0 | A | 90.0 | A | 49.5 | A | 38.5 | N |
| *Plagiochila asplenioides* | 42.0 | N | | | | A | 96.0 | A | 232.0** | A | | | 80.0 | - | 60.5 | A | 40.0 | A |
| *Scapania aspera* | 65.0* | - | 57.0 | - | 44.0* | - | 79.0 | - | 264.0** | A | 153.0** | - | 118.5** | - | 50.5 | + | | |

**Lichens**

| | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Cladonia arbuscula* | 44.0 | A | | | 36.0 | - | 110.5* | - | 252.0** | - | 136.5** | A | 75.0 | A | 55.0 | A | 60* | A |
| *Cladonia pocillum* | 57.5 | - | 54.0 | - | 32.0 | - | 108.0* | A | 192.0 | A | 126.0* | - | 80.5 | - | 60.5 | | | |
| *Cladonia subrangiformis* | 55.0 | + | 75.0** | A | 45.0** | A | 132.0** | A | 288.0** | A | 143.0** | A | 105.0** | A | 66.0 | A | 60* | A |
| *Coelocaulon aculeatum* | 51.5 | - | 74.0** | - | 33.0 | - | 84.0 | A | 206.5 | -/+ | 112.5 | - | 72.5 | -/+ | 57.0 | - | 36.5 | u |

abundance to be significantly different between the two surveys. The only species to show an increase was *Carex panicea. Ditrichum flexicaule* was now absent from the relevés, with *Euphrasia rostkoviana, Scapania aspera, Thymus praecox* subsp. *arcticus* and *Viola rupestris* having decreased in abundance.

**Nodum 2: Nodum with *Rhytidium rugosum***

The CANOCO Monte Carlo simulation demonstrated a significant difference in vegetation composition between the two surveys for this nodum. Six species had also shown a significant change: *Festuca ovina* had increased in abundance, *Cladonia subrangiformis* and *Racomitrium canescens* were now absent in this nodum, with *Coelocaulon aculeatum, Ditrichum flexicaule* and *Thymus praecox* subsp. *arcticus* having decreased.

**Nodum 3 : Nodum typicum of β nodal group with *Minuartia verna***

In this nodum there was no overall difference in vegetation composition between the two surveys. Eight species had however changed significantly. *Gentianella amarella* was the only species to have increased in abundance with no new species recorded. Species that had decreased were: *Racomitrium lanuginosum, Scapania aspera, Selaginella selaginoides, Thymus praecox* subsp. *arcticus, Euphrasia rostkoviana* and *Racomitrium canescens. Cladonia subrangiformis* was now absent.

**Nodum 4: Nodum with *Calluna vulgaris***

The Monte Carlo simulation demonstrated a significant difference in vegetation composition between the two surveys for Nodum 4. There were significant changes in 19 species out of 103 (the number recorded in both surveys) the highest proportion for any nodum under study. Most notably, *Agrostis vinealis* and *Anemone nemorosa* were newly recorded, with *Agrostis capillaris, Anthoxanthum odoratum* and *Calluna vulgaris* having increased in abundance. Species that had decreased included *Briza media, Campanula rotundifolia, Carex panicea, Galium sterneri and Hypnum cupressiforme* var. *lacunosum. Agrostis* *stolonifera*, *Cladonia pocillum*, *C. subrangiformis* and *Rhytidiadelphus loreus* were now absent.

**Nodum 5: Nodum with *Plantago lanceolata***

In Nodum 5, there was a significant difference in vegetation composition between the two surveys. 18 species had changed significantly out of a total of 123 recorded. There were no new species, but *Agrostis capillaris* and *Hieracium pilosella* had increased. Species that had decreased included *Campanula rotundifolia*, *Danthonia decumbens*, *Euphrasia rostkoviana* and *Linum catharticum*. *Plagiochila asplenioides* and *Scapania aspera* were now absent.

**Nodum 6: Nodum typicum of $\chi$ nodal group with *Kobresia simpliciuscula***

In Nodum 6, ten species had changed significantly, but there was no overall difference in the composition of the vegetation. All of these ten species had either decreased or were now absent compared to the original survey. Species that had decreased were: *Cladonia pocillum*, *Ctenidium molluscum*, *Selaginella selaginoides*, *Carex capillaris*, *Euphrasia rostkoviana*, *Koeleria macrantha*, *Scapania aspera*, and *Thymus praecox* subsp. *arcticus*. *Cladonia arbuscula* and *C. subrangiformis* were both absent.

**Nodum 7: Nodum with *Primula farinosa***

Twelve species had changed significantly in Nodum 7. There were no new or increased species. There was, however, an overall difference in vegetation composition. Species that had significantly decreased were: *Carex capillaris, C. hostiana*, *Hypnum cupressiforme* var. *lacunosum*, *Potentilla erecta*, and *Tortella tortuosa*. *Ctenidium molluscum*, *Ditrichum flexicaule*, *Fissidens adianthoides*, *Scapania aspera*, *Selaginella selaginoides* and *Thymus praecox* subsp. *arcticus* had also decreased. *Cladonia subrangiformis* was now absent.

**Nodum 21: Nodum with *Carex caryophyllea***

Only three species out of the 116 recorded had changed significantly in this nodum: *Carex caryophyllea*, *Euphrasia rostkoviana* and *Thymus praecox* subsp. *arcticus* that had all decreased since the original survey. As would be expected from so few significant changes in abundance of individual species, there was no significant difference in overall vegetation composition between the two surveys.

**Nodum 33: Nodum with *Danthonia decumbens***

Nodum 33 had nine species that had changed significantly out of 94 recorded. There was also an overall difference in vegetation composition, as determined from the Monte Carlo simulation. *Thymus praecox* subsp. *arcticus* was newly recorded, and *Hylocomium splendens* had increased. *Danthonia decumbens*, *Dicranum scoparium*, *Hypnum jutlandicum* and *Pleurozium schreberi* had decreased, with *Carex pilulifera*, *Cladonia arbuscula* and *C. subrangiformis* now absent.

**Bare ground**

The proportion of bare ground occurring in all the noda was unchanged. This is especially interesting in Noda 1 and 2 on the sugar limestone where apparently colonisation can keep pace with any vegetation loss due to erosion.

**The Teesdale "rarities"**

As will have become clear from the results presented above, few of the so called "Teesdale rarities" have changed significantly in frequency or abundance between the two vegetation surveys. *Viola rupestris* has already been mentioned as having decreased in abundance in Nodum 1, but had not significantly changed in abundance in the other seven noda in which it was recorded. *Carex pulicaris* had significantly decreased in two of the six noda in which it was previously recorded and *C. capillaris* had also significantly decreased in two out of nine noda. *Selaginella selaginoides* had significantly decreased in all five noda in which it was previously recorded.

In contrast however, *Primula farinosa* had not significantly changed in abundance in any nodum. Other rarities had not changed significantly in any noda, but there was an overall trend in the noda in which they were recorded, for example *Gentiana verna* had decreased in five out of seven noda. In contrast, *Kobresia simpliciuscula* was newly recorded or had increased in six out of eight noda. *Polygala amarella* and *Potentilla crantzii* were absent from the three and four noda, respectively, in which they had been previously recorded.

## 3.4 Discussion

### Nodum 1

It was interesting to note that in Nodum 1 there was no overall change in vegetation composition between the two surveys. One of the reasons for selecting the noda on the sugar limestone soils was the predicted potential, in terms of gap invasion, for species change. It is perhaps surprising that for Nodum 1 at least this was not seen. However the significant decrease in *Thymus praecox* subsp. *arcticus* is of interest. The dramatic change in abundance of this species across many of the noda studied is discussed more fully in Chapter 4. In Nodum 1 specifically it is also worth noting the decline in *Viola rupestris*. This decline is repeated across most of the noda in which the species was recorded, although changes did not reach the level of significance. Clearly if this represented a long-term decline of such a "flagship species" in Teesdale, this would be a source of concern.

### Nodum 2

In contrast to the vegetationally similar Nodum 1, a significant change in overall vegetation composition was recorded. Five out of the six species that had significantly changed had decreased in abundance. Two of these species were mosses, and two lichens. The calcicole *Ditrichum flexicaule* had decreased, but also *Racomitrium canescens*, which is less pH-specific in its habitat requirements. Equally, among the lichen species that had decreased are the calcicole *Cladonia subrangiformis* and *Coelocaulon aculeatum*, more often associated with acid heath.

**Nodum 3**

There was no significant difference in vegetation composition between the two surveys in Nodum 3. The one species to have recorded an increase, *Gentianella amarella* is a biennial. Local abundance of this species will fluctuate seasonally, dependent on the success in previous years of seed production and seedling recruitment. Hence comparing "snapshot" records from two surveys each carried out over only one or two seasons is virtually meaningless. The seven species that have declined include two mosses, one liverwort and one lichen species. As for Nodum 2 there seems to be no trend in the decline in terms of pH preference, for example the calcicole *Scapania aspera* has decreased, as have *Racomitrium canescens* and *Euphrasia rostkoviana*, which are tolerant of a wide pH range, and also the generally calcifuge *Racomitrium lanuginosum*.

**Nodum 4**

The vegetation composition of Nodum 4 has significantly changed between the two surveys. The majority (13 out of 19) of the species that have changed have decreased in abundance or are now absent, with grass and sedge species strongly represented. The most obvious key to understanding the change in vegetation composition in this nodum is with regard to the significant increase in cover of the dominant species, *Calluna vulgaris.* Jones (1973) mentioned a possible increase in *Calluna* cover in the limestone heath from evidence from previous aerial photographs (not obtainable) compared to the set taken in October 1969 and used for production of the vegetation maps. The same comparison can be performed using these 1969 photographs compared to a contemporary series from August 1995.

Selected photographs from the 1969 and 1995 aerial surveys are reproduced in Plates 3.1-3.4. Plates 3.1 and 3.2 correspond to the area marked "A" on the overlay to the 1:100000 scale vegetation map of the fell (in thesis pocket) and Plates 3.3 and 3.4 correspond to the area marked "B" on the overlay to the same map. Area "A" is covered in more detail by the vegetation maps Sheets 3-5 and area "B" is covered by Sheet 1.

**Plates 3.1-3.4 Aerial photographs of Widdybank Fell from October 1969 (Plates 3.1 & 3.3) source: Meridian Airmaps Ltd, Lancing, Sussex and August 1995 (Plates 3.2 & 3.4) source: NERC. Lighter areas of vegetation on each plate are grassland, darker areas are dominated by *Calluna vulgaris*.**

Plate 3.1 Composite photograph from 1969 (approx. scale 1:75000) along the sugar limestone outcrop. The region shown corresponds to the area marked "A"on the overlay to the 1:10000 scale vegetation map of the fell (in thesis pocket).

Plate 3.2 Photograph from 1995 (approx. scale 1:75000) showing the same region as above, with an additional area showing the relative position of the reservoir.

Plate 3.3 Photograph from 1969 (approx. scale 1:50000) showing a Nodum 4/5 and 33 complex of vegetation on the Robinson Limestone plateau (centre). The region shown corresponds to the area marked "B" on the overlay to the 1:10000 scale vegetation map of the fell (in thesis pocket).

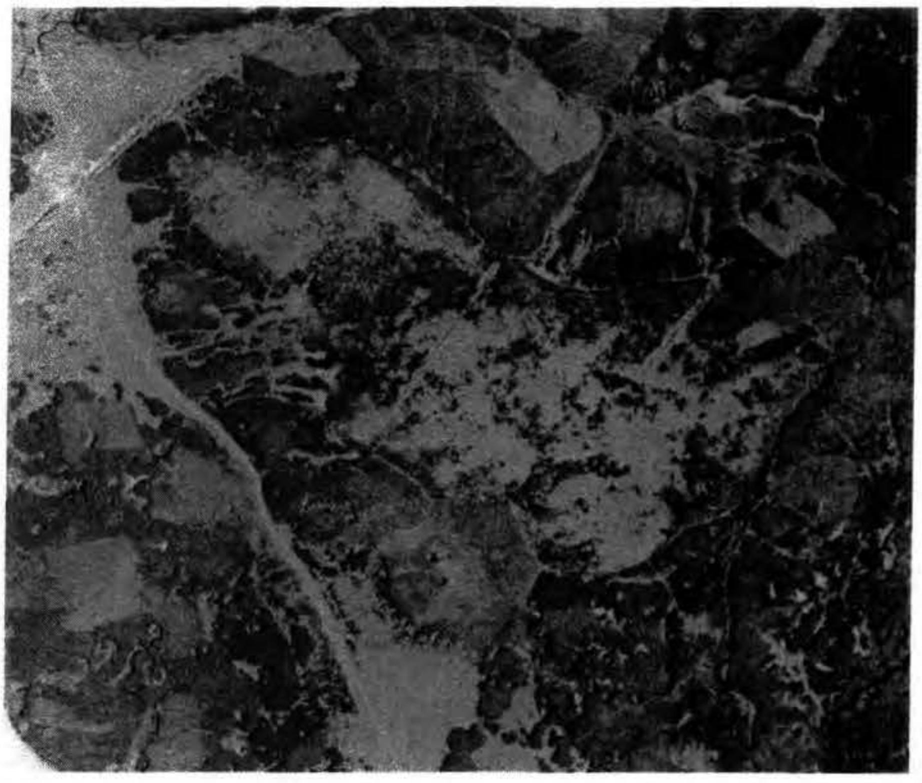


Plate 3.4 Photograph from 1995 (approx. scale 1:50000) showing the same region as above. The regular-sided light patches are where the *Calluna* has been recently burnt.

Plates 3.1 and 3.2 include the area from which all Nodum 4 relevés were obtained in both surveys. The extent of *Calluna* cover has increased on some of the grass/heath boundaries since 1969. However a more obvious change can be seen by comparing Plates 3.3 and 3.4. These show *Calluna* cover in a Nodum 4/5 and 33 complex region. Here it is not the extent of *Calluna* that has changed, but rather the density of existing *Calluna* stands. This implied that an increase in size of relatively mature bushes was responsible, rather than seedling recruitment. A search of this area in November 1998 found very few seedlings, but instead that prostrate shoots from mature bushes had often formed adventitious roots.

The increase in *Calluna* cover, and consequently increased production of its litter, which is acid (Gimingham, 1960), could be responsible for the decline in calcicole species, namely *Galium sterneri* and *Hypnum cupressiforme* var. *lacunosum*. Many of the species that have decreased are, however, less specific in their pH requirements, for example, *Briza media* and *Campanula rotundifolia*, but it is possible that these species are affected by either the allelopathic secretions of *Calluna* (Gimingham, 1975) or by the increased shading. Certainly available data suggests that *Briza* and *Carex panicea* are shade intolerant although *Campanula* is probably tolerant. One of the newly recorded species, *Anemone nemorosa,* is shade tolerant (Grime, Hodgson & Hunt, 1988).

The *Calluna* increase in Nodum 4 is not as a result of regeneration following burning as this has not occurred on the areas of limestone heath in the recent past (Ian Findlay *pers. comm.*) although it has occurred in other *Calluna* stands on the fell, as evident in Plate 3.4. A change in grazing pressure might be indicated, which is discussed in Chapter 6. The effects of a reduction in grazing pressure might be most clearly observed in areas of heathland, as these are the areas most lightly grazed by sheep, who have been shown to prefer grassland (Willis, 1995).

**Nodum 5**

There was a significant difference in vegetation composition between surveys in Nodum 5. All but two of the 18 species that have changed have decreased, and forbs, grasses, bryophytes and lichens were all well represented in this group. There is no obvious autecological feature that the species that have declined share except that many are classified by Grime *et al.* (1988) as stress tolerators, for example *Campanula rotundifolia* and *Danthonia decumbens*, or stress-tolerant ruderals, namely *Euphrasia rostkoviana* and *Linum catharticum*. However, as the two latter species are an annual and a biennial, respectively, the same caveats apply when interpreting abundance data as previously stated for *Gentianella amarella*. Nodum 5 also had the largest difference in liverwort abundance between surveys. All three of the species found to be changing in any nodum have significantly decreased or are now absent in this nodum. It is interesting that there was no significant increase in *Calluna vulgaris* cover in Nodum 5, despite the fact that Nodum 4 and 5 often occur as a complex community, and that cover in such a community has apparently increased on the Robinson Limestone (as previously demonstrated). However only one relevé for Nodum 5 was collected in this area so any such change will not have been recorded.

**Nodum 6**

There was no significant change overall in vegetation between the two surveys for Nodum 6. Those individual species that had changed had all decreased or were now absent in the present survey. Seven of these species have a strong preference for soils of high pH (with *Euphrasia rostkoviana*, *Selaginella selaginoides* and *Cladonia arbuscula* the exceptions, tolerant of a wider pH range).

**Nodum 7**

In Nodum 7, a significant overall change in vegetation composition was seen. The species that had changed significantly in abundance had all decreased or were now absent. Five bryophytes and a lichen were represented in this group, out of a total of twelve species. With the exception of *Carex hostiana*, *Fissidens adianthoides* and *Potentilla erecta,* the species that have changed are associated with calcareous soil. This nodum has the wettest soils of the noda studied, but there is no obvious pattern of species change that could be attributed to a change in moisture availability.

### Nodum 21

Although no significant vegetation change was recorded overall in Nodum 21 it is worth noting that *Carex caryophyllea*, the differential species, has decreased. Also *Thymus praecox* subsp. *arcticus* has decreased in this nodum i.e. the same decline has been observed in this nodum on unaltered limestone, as seen in the noda on the sugar limestone.

### Nodum 33

There was a significant difference in vegetation composition between the two surveys for Nodum 33. The differential species *Danthonia decumbens* has decreased, and interestingly *Thymus praecox* subsp. *arcticus* was newly recorded, in sharp contrast to the decline seen on the limestone grasslands. Six mosses and two lichen species were among the nine species for which changes were detected. There was no clear pattern in terms of pH preference in the species changing in abundance. Some of the differences recorded in this nodum may be a result of noticeably different sub-types of grassland classified as Nodum 33. Some areas are of coarse grassland which are relatively species-poor and dominated by species such as *Juncus squarrosus* and *Galium saxatile*, for example relevé 828. Others regions such as relevé 830 in the large area of Nodum 33 by the gate to the Birkdale track comprise less coarse, more species-rich grassland, which include species like *Achillea millefolium*, *Trifolium repens* and *Thymus*. It is possible that there was a bias in collection of relevés in the original survey to the species-poor sub-type. Unfortunately, too few of these positions could be located with accuracy sufficient to confirm or deny this. Hence results from this nodum have been assessed with these factors in mind.

### The Teesdale "rarities"

None of the changes described in abundance of the Teesdale "rarities" give particular cause for concern. Few of the species had changed significantly in abundance in many noda in which they were recorded. Despite trends across several noda, e.g. the apparent decline in *Gentiana verna*, none of the changes for this species reached the level of significance. Future monitoring of these species is, however, a worthwhile undertaking.

### 3.5 Conclusions

The null hypothesis of no change in the vegetation of Widdybank Fell since 1969 has been rejected. This follows the evidence for significant change in the composition of the vegetation in five out of nine selected noda between the present and original surveys. Some species groups (e.g. grasses) may be over-represented among the species that have significantly changed in abundance. Additionally species traits have been identified (for example pH preference) which may be shared by the species that have changed. Chapter 4 continues this investigation.

In the future, a number of different methods of vegetation monitoring would be recommended. To identify any large-scale changes, resurveying of the (permanently marked) quadrats used in this thesis at 5-10 year intervals would be useful. This would increase the value of the surveys of Jones (1973) and the present survey, as data collected over a series of time points is clearly more robust in detecting long-term vegetation changes. Repeating this survey will be of benefit to monitor relatively large-scale changes in the vegetation. As for the present survey it will be important to take into account seasonal changes in the vegetation and recheck the quadrats several times in a season. Repeating the aerial photography of the fell would also be useful for monitoring any changes in the grass-heath boundary and in heather density and cover.

In order detect more subtle changes in vegetation composition, point quadrat studies similar to that of Maxwell (1997) would be of particular use. The sites used for Maxwell's study, all located within Nodum 4, were permanently marked so could be re-assessed, preferably in mid-June or mid-late July (the two survey dates originally used). Another recent survey, of *Achillea millefolium* distribution and abundance in Nodum 4 (Scott, 1997) also left marked quadrats which could be re-assessed as part of a general vegetation survey. Population dynamic studies of particular species like those of Doody (1975) again using marked plots, but following the fate of individual plants (methods summarised in Bradshaw, 1981) could also be used. These sites were marked by means of buried metal rods, and 84 % of them have been recently relocated (Margaret Bradshaw *pers. comm.*) so the benefit of repeating the work after c. 25 years may be considerable. It would be of particular use to remonitor species such as *Polygala amarella* which occur at very low frequency in the grasslands, and whose populations may fluctuate quite considerably from year to year (Doody, 1975).

### *3.6 Summary*

- The null hypothesis that there has been no change in the vegetation of Widdybank Fell since a survey of 1967-1969 by Jones (1973) was tested by comparing data from this original survey with that collected in a present-day survey, focusing on nine vegetation noda on the fell.

- This null hypothesis was rejected as there have been significant changes in community composition in five out of these nine noda since the survey of Jones. For all nine noda more individual species had significantly decreased in abundance than had increased. The most notable change in any species was the significant decrease in abundance of *Thymus praecox* subsp. *arcticus* in seven of the noda on calcareous soils, with the species newly recorded in the acid grassland, Nodum 33. There had, however, been few changes in frequency or abundance of the Teesdale "rarities" between the two vegetation surveys.

# 4. Examination of species ecological and physiological traits

## 4.1 Introduction

As a result of investigations reported in the previous chapter, the null hypothesis of no change in the vegetation of Widdybank Fell since 1969 has been rejected. The present chapter investigates these changes further by examining characteristics of species and groups of species across all nine noda under study.

Firstly, the species that have changed across several noda are listed to provide a context for the chapter. Next there is an investigation to see if any particular group of species (such as grasses or lichens) contained more species that had significantly changed between surveys than would be expected, given the group's relative size as a component of the flora. This is tested as a null hypothesis i.e. that there is no difference between the observed and expected distribution of the significantly changed species among the species groups. Then there follows an examination of whether the individual species that had been found to change in abundance between the surveys shared any particular physiological or ecological traits, compared to the flora of the nine noda as a whole. For example, within the trait of longevity, whether such species were more likely to be annuals rather than perennials or biennials. The null hypothesis for each trait was thus that the species that had changed in abundance between the two surveys did not share a particular feature within a particular physiological trait compared to the flora as a whole.

The following traits were selected for detailed investigation:

- Floristic element number
- Longevity
- Regenerative strategy
- Leaf phenology
- Flowering time and duration

- C-S-R strategy
- nuclear DNA content
- Reaction Value
- Nitrogen Value

These traits are described in more detail below. Data were only available or relevant for angiosperms, unless otherwise stated.

**Floristic element number (Preston & Hill, 1997; Hill & Preston, 1998)**

As already described in Chapter 2, British vascular plants have been classified into floristic elements according to their geographical range in the Northern Hemisphere, based firstly on latitudinal and then on longitudinal categories (Preston & Hill, 1997). The same classification has also been used for bryophytes (Hill & Preston, 1998).

**Longevity (Clapham, Tutin & Moore, 1987; Grime *et al.*, 1988)**

This refers to whether a species is annual, completing its life cycle in one growing season, or biennial, taking two seasons, or perennial, living for more than two seasons.

**Regenerative strategy (Grime *et al.*, 1988)**

Species were classified by Grime *et al.* according to their predominant strategies for regeneration. Such strategies include clonal (vegetative) expansion or production of seed.

**Leaf phenology (Grime *et al.*, 1988)**

This is a measure of the seasonal duration of the leaf canopy throughout the year i.e. at what times the plant is photosynthetically active.

**Flowering time and duration (Grime *et al.*, 1988)**

This is the time of first flowering and its subsequent duration. Both leaf phenology and flowering time depend on local climatic conditions. Species at

Widdybank may actually flower later than their given date because with increased altitude, the growing season is shortened and starts later (see Chapter 7). However, in the absence of such site-specific information, the standard dates given by Grime were still used.

**C-S-R strategy (Grime *et al.*, 1988)**

C-S-R strategy is a model devised by Grime (1977) that classifies plant species according to their presence or absence under growth conditions of "stress" or "disturbance". "Stress" is defined as conditions limiting photosynthetic production, such as drought. "Disturbance" is defined as conditions resulting in destruction of plant biomass, for example through grazing or frost damage. Three primary plant strategies are recognised: Competitors (C) are found in conditions of low stress and disturbance. Stress tolerators (S) grow under conditions of high stress and low disturbance. Ruderals (R) are found in conditions of low stress and high disturbance. No species can tolerate both high stress and high disturbance; the fourth option.

**Nuclear DNA content (Grime *et al.*, 1988) -used to calculate standardised nuclear DNA content (see below).**

The relative amount of nuclear DNA in cells of plant species common in northern England has been found to correlate with the timing and rate of plant shoot growth in the spring (Grime & Mowforth, 1982). Two major strategies for shoot phenology have emerged, apparently depending on the climatic conditions under which the species evolved. Some species have a small cell size and low nuclear DNA amount that allows a relatively short cell-cycle and rapid growth in warm conditions. The penalty of this strategy is delayed growth under cold spring conditions. An example of such a strategist is *Cardamine pratensis*, which has a nuclear DNA content of 3.3 pg. The second group of strategists are able to produce rapid spring growth by the expansion of large cells with large nuclei, differentiated but not expanded in the previous season. The growth of such strategists tends to slow down towards the end of the summer because of the longer cell-cycle (Bennett, 1971) and the focus on producing cells for expansion in the next season. Many grasses fall into this category, for example *Briza media* with nuclear DNA content of 16.9 pg.

**Standardised nuclear DNA content data from (Grime *et al.*, 1988).**

In order to discern inter-specific differences in nuclear DNA content it is necessary to first correct for phylogenetic trends. Hence for comparative purposes, nuclear DNA content for each species was standardised according to the mean content for their family. This was in order to determine if species with relatively high or low contents for the family had changed. Content for each species was standardised thus:

$$\frac{\text{nDNA content for the species - average nDNA content for the family}}{\text{standard deviation for the family}}$$

The list of families and their mean nDNA content is in Appendix C, Table (i).

**Reaction Value (Ellenberg, 1988)**

Reaction value is a scale of the pH of soils in which a species is typically found, from 1 (extreme acidity) to 9 (highly calcareous). The scale is reproduced in Appendix C and was used to score the angiosperm species from the surveys. Data for bryophytes and lichens on this scale are not available, but these have been classified as A (generally associated with acid soils), C (generally associated with calcareous soils) and I (intermediate, usually tolerating a wide pH range, or associated with neutral soils). Descriptions of preferred habitat are from Smith, (1980) and Watson (1968) for bryophytes and Purvis *et al.* (1992) for lichens.

**Nitrogen Value (Ellenberg, 1988)**

Nitrogen value is a scale of species occurrence at different levels of available soil nitrogen from 1 (low availability) to 9 (high availability). The scale is reproduced in Appendix C.

## 4.2 Methods

### *4.2.1 Species that had changed in frequency or abundance across several noda*

Species that had significantly changed in frequency or abundance in more than one nodum were extracted from the data and listed.

### *4.2.2 Analysis of species groups*

Each species occurring in either survey was classified into one of four categories, depending on their predominant trend for change across all nine noda:

1. Species that had significantly changed in at least one nodum by having increased or being newly recorded.
2. Species that had significantly changed in at least one nodum by having decreased or being now absent.
3. Species that had changed in an ambiguous way i.e. significantly increased in some noda but significantly decreased in about the same number of other noda. (The number of species changing ambiguously was remarkably few, with good consistency across the noda in the direction of change).
4. Species that had not significantly changed in any nodum.

For each of the five major groups of species (forbs and shrubs, grasses sedges and rushes, mosses, liverworts and lichens) the total number of species (from all noda) that had significantly changed in abundance in the Mann-Whitney tests were noted (Table 4.1). For initial analysis, numbers of species having increased, decreased or changed ambiguously were combined. The expected distribution of these significantly changed species among the five species groups was calculated, taking into account the total number of species (significantly changed plus not significantly changed) recorded for each category.

**Table 4.1 Summary data (extracted from Table 3.3 and Table (iii) in Appendix B) for groups of species across the nine noda.**

| | Forbs and shrubs | Grasses, sedges and rushes | Mosses | Liver-worts | Lichens | Total |
|---|---|---|---|---|---|---|
| Total number of species recorded across the nine noda by Jones (1973). Within this total, the number of species only found in this survey are given in brackets | 57 (12) | 29 (6) | 49 (20) | 12 (8) | 20 (6) | 167 (52) |
| Total number of species recorded across the nine noda in the present survey. Within this total, the number of species only found in this survey are given in brackets | 54 (8) | 26 (2) | 34 (2) | 4 (0) | 19 (5) | 137 (17) |
| Total number of species recorded across the nine noda in both surveys | 66 | 31 | 54 | 12 | 25 | 188 |
| Number of species new or significantly increased between surveys | 5 | 4 | | | | 9 |
| Number of species absent or significantly decreased between surveys | 8 | 10 | 10 | 3 | 4 | 35 |
| Number of species significantly changed between surveys in either direction, or ambiguously | 13 | 15 | 12 | 3 | 4 | 48 |

A chi-squared goodness-of-fit test was used to test the null hypothesis that there was no difference between observed and expected distribution of the significantly changed species among the species groups. Use of this test is only considered appropriate when sample sizes are sufficient such that no expected value is less than five (e.g. Devore & Peck, 1993). To satisfy this criterion, mosses and liverworts were amalgamated to form one category. The test thus examined distribution between four groups. It would clearly also have been desirable to perform separate chi-squared tests on species that had significantly increased and species that had significantly decreased. In practice however, numbers were only sufficient to perform separate tests for species having decreased and for this test it was additionally necessary to amalgamate bryophyte and lichen data so that the test examined distribution between three groups.

### *4.2.3 Investigation of species ecological and physiological traits*

Each individual species occurring in the nine noda in either survey had previously been classified into one of four categories depending on any change between surveys (Section 4.2.2). Additionally, each species was assigned to its correct category for each of the physiological/ecological traits listed in Section 4.1. With one exception, all the data for ecological and physiological traits fell into discrete categories. For the exception, standardised nDNA content, two data categories were established, where standardised content was more than average for the family and where it was less than average.

For each trait, the number of species significantly changing in abundance was counted (at this stage numbers of species having increased, decreased or changed ambiguously were pooled). The expected distribution of these significantly changing species among the categories of each trait was calculated, taking into account the total number of species recorded for each category. A chi-squared goodness-of-fit test was used to test the null hypothesis that there was no significant difference between the observed and expected distributions of the significantly changing species among the categories of each trait. In order that no expected value was less than five, trait categories were amalgamated where necessary (see Results, Table 4.3, later). Chi-squared analysis could not be performed for species longevity or leaf phenology because both traits were dominated by one category, perennial and always evergreen, respectively.

As for groups of species, it was desirable to perform separate chi-squared tests on species that had increased significantly and those that had decreased significantly. In practice, however numbers were only sufficient to perform separate tests for species having decreased, and even this separation was not possible for standardised nDNA content.

The tests for soil pH preference were carried out in a different way. Rather than using the combined data set from all noda, Noda 1-3, 5-7 and 21 (calcareous grasslands) were examined separately from Noda 4 and 33 (limestone heath and acid grassland, respectively). In addition, the chi-squared tests were solely performed for species that had decreased. So few species that had increased were recorded that combining these data would have been meaningless.

## 4.3 Results

### 4.3.1 Species groups

**Forbs and shrubs**

A total of 13 forb or shrub species had changed significantly in frequency or abundance or both in at least one nodum, five new or having increased and eight absent or having decreased. Five of these 13 species had changed in several noda. *Campanula rotundifolia* had significantly decreased in Noda 4 and 5, *Euphrasia rostkoviana* had decreased in Noda 1, 3, 5, 6 and 21, *Potentilla erecta* has decreased in Noda 4, 5 and 7 and *Selaginella selaginoides* had decreased widely, in Noda 3, 4, 5, 6 and 7. Most strikingly, *Thymus praecox* subsp. *arcticus* had decreased in abundance in Noda 1, 2, 3, 5, 6, 7 and 21, (but maintained a high frequency in all these noda) was unchanged in Nodum 4, but was newly recorded in Nodum 33.

### Grasses, sedges and rushes

Fifteen grass, sedge or rush species had changed significantly in frequency or abundance between the two surveys in at least one nodum. Four species were new or had increased and ten had decreased or were now absent, with *Carex panicea* having increased in Nodum 1, but decreased in Nodum 4. *Agrostis capillaris* had increased in both Noda 4 and 5. Species that had significantly decreased in two noda were *Carex capillaris* in Noda 6 and 7, *C. pulicaris* in Noda 4 and 5 and *Danthonia decumbens* in Noda 5 and 33, a species that has declined strongly in frequency across these two noda but maintained similar abundance within individual relevés.

### Mosses

There was a considerable loss of moss diversity between the two vegetation surveys, from 42 species recorded by Jones (1973) to 34 in the present survey. Twelve species of moss had significantly changed in frequency or abundance between the two surveys. Ten of these species had decreased or were now absent, but of the remaining two, *Hylocomium splendens* had increased in abundance but decreased in frequency, and *Dicranum scoparium* had increased in Nodum 5, but decreased in Nodum 33. Including *Dicranum scoparium*, six of the significantly changing species had changed in more than one nodum. All the following had decreased: *Ctendium molluscum* in Noda 6 and 7, *Hypnum cupressiforme* var. *lacunosum* in Noda 4 and 7, and *Racomitrium lanuginosum* in Noda 3 and 4. *Ditrichum flexicaule* had significantly decreased in Nodum 2 and was now absent in Nodum 1. *Racomitrium canescens* had decreased in Nodum 3 and was now absent from Nodum 2.

### Liverworts

As seen for mosses, the number of liverwort species had also declined; from 20 in the survey of Jones (1973) to only 4 in the present survey. Three species had changed significantly in frequency or abundance between surveys and were now absent or had decreased. Only *Scapania aspera* had changed significantly in more than one nodum, recording a significant decline in Noda 1, 3, 5, 6 and 7 and now completely absent in Nodum 5. The decline has been most noticeable in frequency of occurrence in relevés rather than dramatic changes in median Domin score between the two surveys.

**Lichens**

Out of a total of 25 lichen species recorded in the two surveys, four had changed significantly in frequency or abundance, all now absent or having declined. *Coelocaulon aculeatum* had decreased in Nodum 2 but the other three had changed in more than one nodum: *Cladonia arbuscula* had significantly decreased in Noda 4 and 5 and was now absent in Nodum 6, *C. pocillum* had decreased in Nodum 6 and was now absent in Nodum 4 and most strikingly, *C. subrangiformis* was absent in seven noda in which it was previously recorded: Noda 2, 3, 4, 5, 6, 7 and 33.

### *4.3.2 Results for groups of species*

The null hypothesis that had been tested for the groups of species was that there was no difference between the observed and expected distribution of the species that had significantly changed between these groups. This null hypothesis was rejected (see Table 4.2) as the calculated $\chi^2$ of 8.47 was greater than the critical value of $\chi^2$ of 7.81 ($P \leq 0.05$, 3 degrees of freedom). The individual species group making by far the largest contribution to the overall $\chi^2$ value was grasses, sedges and rushes with a $\chi^2$ of 6.78. When just species that had decreased were tested the result was not significant however; $\chi^2$ was 4.59 with the critical value of $\chi^2$ at 5.99 for two degrees of freedom.

### *4.3.3 Investigation of ecological and physiological traits of species*

Table (ii) in Appendix C gives the raw data for the ecological and physiological traits of the species encountered in the two surveys and their predominant change in abundance between surveys. Table 4.3 provides details of the individual chi-squared tests performed on the distribution of significantly changed species among the categories of each trait. From Table 4.3 it can be seen that only two of the chi-squared tests were significant, both where $P \leq 0.05$, for C-S-R strategy

**Table 4.2 Chi-squared analysis of the distribution of significantly changed species among the different species groups.**

| | **Part A: species that have increased and decreased, combined** | **Part B: species that have decreased** |
|---|---|---|
| Species groups (amalgamated where necessary so no expected value in chi-squared test is <5 ) | forbs and shrubs<br><br>grasses, sedges and rushes<br><br>mosses and liverworts (amalgamated)<br><br>lichens | forbs and shrubs<br><br>grasses, sedges and rushes<br><br>mosses and liverworts and lichens (amalgamated) |
| Total number of observations | 188 | 188 |
| Total number significantly changed (Part A) or decreased (Part B) | 48 | 35 |
| Observed number of significantly changed/decreased species for each category (same order as categories) | 13, 15, 15, 4 | 8, 10, 17 |
| Expected number of significantly changed/decreased species | 16.5, 7.75, 16.5, 6.25 | 12.29, 5.77, 16.94 |
| Calculated $\chi^2$ | 8.47 | 4.59 |
| Critical value of $\chi^2$ ($P \leq 0.05$) | 7.81 | 5.99 |

**Table 4.3 Chi-squared analyis of ecological and physiological traits shared by significantly changed species at Widdybank compared to the flora of the nine noda as a whole.**

**Part A Species that have increased and decreased in abundance, combined.**

| | **Biome categories** | **Regenerative strategy** | **Flowering time and duration** | **CSR strategy** | **Standardised nDNA content** | **Nitrogen Value** |
|---|---|---|---|---|---|---|
| Categories (amalgamated where necessary so no expected value in chi-squared test is <5 ) | 10, 20, 30<br>40, 50<br>60, 70, 80 ,90 | (V)?B, (V)B, ?B, B(V), BV, V?B<br>?S, S, SB, SBV, SV, W, WB<br>V, V?S, VB, VS, VS?B, VW | early (Mar 3 to May 2)<br>mid (May 3 to Jun 3)<br>late (Jun 4 to Aug 3) | S<br>SR, S-SR, S-CSR, S-CS, SC, SR-CSR<br>CR, CR-CSR, CSR, R-CSR | standardised contents less than the average for the family (i.e. negative)<br>standardised contents more than the average for the family (i.e. positive) | 1 & 2<br>3 & 4<br>5, 6, 7 & x |
| Total number of observations | 156 | 64 | 61 | 64 | 44 | 73 |
| Total number significantly changed | 43 | 21 | 22 | 21 | 14 | 24 |
| Observed number of significantly changed species for each category (same order as categories) | 5, 20, 18 | 5, 7, 9 | 6, 8, 8 | 12, 8, 3 | 10, 4 | 15, 4, 5 |
| Expected number of significantly changed species | 8.82, 18.19, 15.99 | 6.23, 5.25, 9.52 | 6.49, 8.30, 7.21 | 7.22, 6.89, 6.89 | 8.27, 5.73 | 10.52, 6.25, 7.23 |
| Calculated $\chi^2$ | 2.09 | 0.86 | 0.13 | 5.54 | 0.88 | 3.40 |
| Critical value of $\chi^2$ ($P \leq 0.05$) | 5.99 | 5.99 | 5.99 | 5.99 | 3.84 | 5.99 |

**Part B Only species that have decreased in abundance.**

| | Biome categories | Regenerative strategy | Flowering time and duration | CSR strategy | pH (noda with calcareous soils only) | pH (noda with acid soils only) | Nitrogen Value |
|---|---|---|---|---|---|---|---|
| Categories (amalgamated where necessary so no expected value in chi-squared test is < 5) | 10, 20, 30<br>40, 50<br>60, 70 ,80 ,90 | (V)?B, (V)B, ?B, B(V), BV, V?B<br>?S, S, SB, SBV, SV, W, WBV, V?S, VB, VS, VS?B, VW | early (Mar 3 to May 5)<br>late (Jun 1 to Aug 3) | S<br>SR, S-SR, S-CSR, S-CS, SC, SR-CSR, CR, CR-CSR, CSR, R-CSR | 1, 2 & 3= acid<br>7, 8 & 9= calcareous<br>4, 5 ,6, x= intermediate | acid and calcareous<br>intermediate | 1 & 2, 3<br>4, 5, 6, 7 & x |
| Total number of observations | 156 | 64 | 61 | 64 | 147 | 115 | 73 |
| Total number having decreased | 31 | 12 | 13 | 12 | 27 | 17 | 16 |
| Observed number of significantly decreased species for each category (same order as categories) | 3, 14, 4 | 7 5 | 3 10 | 8 4 | 3, 13, 11 | 8 9 | 14 2 |
| Expected number of significantly decreased species | 6.36, 13.11, 11.53 | 6.56, 5.44 | 5.33, 7.67 | 4.13, 7.88 | 5.32, 7.29 14.39 | 8.43, 8.57 | 10.74, 5.26 |
| Calculated $\chi^2$ | 2.31 | 0.06 | 1.72 | 5.55 | 7.38 | 0.04 | 3.01 |
| Critical value of $\chi^2$ ($P \leq 0.05$) | 5.99 | 3.84 | 3.84 | 3.84 | 5.99 | 3.84 | 3.84 |

and soil pH preference for noda with calcareous soils. These tests were both for species that had decreased only (Part B). The null hypothesis of no difference between observed and expected distributions of the significantly changed species among the categories of a trait is hence rejected for these two traits.

For C-S-R strategy the different categories had been amalgamated into two groups so no expected value in the chi-squared test was less than five. The groups were pure stress-tolerators (S) and all other strategies. More of the significantly decreased species were stress-tolerators than would be expected by chance alone.

For soil pH preference in the noda with calcareous soils (1-3, 5-7 and 21) three groups had been formed for the chi-squared test from the total number of species occurring in these noda. These were species preferring acid conditions (32 recorded in total), species preferring basic conditions (37 recorded in total) and those with a wide pH tolerance (78 species recorded). Hence all three groups were well represented in these noda. The presence of the species preferring acid conditions is probably a result of growth in areas where the soil has become leached. Of the species that had significantly decreased across these noda, more were classified as preferring basic conditions than expected by chance alone.

## 4.4 Discussion

### 4.4.1 Groups of species

Where species have changed in frequency or abundance across several noda and therefore across a considerable spatial scale, this is more likely to be a response to a large-scale environmental factor such as a regional climate change than a more localised effect, such as trampling or sheep rubbing.

**Forbs and shrubs**

All five species that had significantly changed in several noda had declined. The only exception was the newly recorded *Thymus praecox* subsp. *arcticus* in Nodum 33. For *Euphrasia rostkoviana*, an annual species with no buried seed bank (Grime *et al.*, 1988) local abundance can be expected to fluctuate every year, depending on seed dispersal the previous season. Hence any recorded small-scale changes between surveys and even within a single nodum would be of little interest. However, the larger-scale decrease in abundance across several noda could be the result of a longer term decline in the success of this species. A study of yearly population dynamics would be required to confirm this.

*Campanula rotundifolia, Potentilla erecta and Euphrasia rostkoviana* tolerate soils of a wide pH range, but *Thymus praecox* subsp. *arcticus* is generally confined to limestone. This makes its general decrease in abundance in the limestone noda and the new record in the acid Nodum 33 quite surprising, although it is possible that this is a result of recording differences between the two apparent sub-types of vegetation in Nodum 33 as discussed earlier. However an investigation of a possible reduction in pH of the limestone grasslands needs to be carried out. A recent study by Adamson *et al.* (1996) sampled a range of mineral soils at Moor House and Upper Teesdale National Nature Reserves that had been first examined in 1963-1973. Soil acidity had increased over this period, particularly in the organic and A horizons of the soil profile. The most likely cause of this change is the deposition of atmospheric pollutants such as sulphur dioxide, which can result in soil and plant acidification when deposited in rainwater. Upland areas, with high levels of rainfall, can receive much higher doses than lowland regions (Vincent *et al.*, 1996). The role of acid deposition as an environmental change factor at Widdybank Fell is investigated more fully in Chapter 5.

*Campanula*, *Euphrasia*, *Potentilla* and *Thymus* (no data for *Selaginella selaginoides*) are associated with nitrogen-deficient soils, as is the case for a large part of the Widdybank flora. Another trait equally common within the flora is wintergreeness. *Campanula* is wintergreen, *Thymus* an evergreen, and *Potentilla* may retain basal leaves through a mild winter. In terms of C-S-R strategy, *Campanula* and *Thymus* are stress-tolerators, *Euphrasia* is a stress-tolerant ruderal and *Potentilla* is intermediate between a stress tolerator and a C-S-R strategist. The three perennial angiosperms reproduce both vegetatively and via a persistent seed bank. Flowering times are May, June and July for *Thymus*, *Potentilla* and *Campanula*, respectively and for three or four months each. With the exception of soil pH preference, none of the ecological traits shown by these species particularly suggest why they might be declining compared to the flora as a whole.

**Grasses, sedges and rushes**

This group had a disproportionately high number of species that had changed in abundance within it; most of these had decreased in abundance. Graminoids tend to have high nDNA contents and therefore take advantage of an early spring phenology. However six out of eight of the changed species for which nDNA content data are available had a content less than average for the family Gramineae (n= 15). Three of these species had increased in abundance (e.g. *Agrostis capillaris*) and three had decreased (e.g. *Danthonia decumbens*) so this does not aid insight into why these species have been changing in abundance. *Agrostis capillaris* is a C-S-R strategist, whereas *Danthonia decumbens* is a stress tolerator and the species that have changed in abundance tend to be stress-tolerators or have more intermediate strategies.

**Mosses**

Of the 12 moss species that have declined, four are calcicoles and have decreased on the limestone grasslands: *Ctenidium molluscum*, *Ditrichum flexicaule*, *Hypnum cupressiforme* var. *lacunosum* and *Tortella tortuosa*, and three are calcifuge and have decreased in Nodum 33: *Hylocomium splendens* (actually increased in frequency but decreased in abundance), *Hypnum jutlandicum* and *Pleurozium schreberi*. Apparent vegetation changes in Nodum 33 are hard to interpret, given the possibility that the two vegetation surveys sampled different sub-types within the nodum (see Chapter 3). The remainder of the mosses are more catholic in their habitat requirements. The loss of calcicole bryophytes on the limestone grasslands is of particular interest (NB more of such species had decreased than expected by chance in the chi-squared analysis). This could potentially be a result of increased acid deposition from the atmosphere, as described above. Bryophytes could be expected to be especially sensitive as they directly absorb elements from rainwater. In contrast, rainwater absorbed by higher plants has the potential to be chemically modified by the soil before uptake. Bryophytes are also drought sensitive, so it is clearly worth investigating rainfall patterns over the years of the two surveys to examine whether this might be the cause of the general decrease in abundance.

**Liverworts**

Only *Scapania aspera* has significantly changed in more than one nodum, and has significantly decreased in abundance or is now absent in five noda. This species is generally confined to calcareous habitats. The reasons for its decline may be the same as stated for the mosses above, namely acid deposition or drought.

**Lichens**

Of the three lichens that have declined in several noda, *Cladonia arbuscula* and *Coelocaulon aculeatum* are associated with acid substrates and *Cladonia subrangiformis* calcareous substrates. All have declined in noda with both acid and calcareous soils, so substrate type is apparently not related to this change. The decline of these species in Nodum 4 could potentially be explained by the increase in density of *Calluna vulgaris* stands. Lichens on acid heath favour open *Calluna* stands (Purvis *et al.*, 1992), so any increased shading may have been unfavourable. Disturbance through grazing or trampling is also important in the maintenance of species in calcareous grasslands (Purvis *et al.*, 1992). Hence any general reduction in grazing pressure could be responsible for the effects seen. Lichens are sensitive to atmospheric pollution; in the same way as bryophytes they directly absorb elements from rainwater. Hence any change in rainwater chemistry could be of importance.

### *4.4.2 Species ecological and physiological traits*

The disproportionately high decline in stress-tolerant species across the nine noda is interesting. This implies that some local or larger-scale amelioration of growth conditions may have occurred, with the result that a stress-tolerant strategy (with accompanying low relative growth rate) has become less successful. Climatic amelioration resulting in a more favourable growing season could have been produced by the presence of the reservoir or by changes in the regional climate. Alternatively soil nutrient deficiency might have been reduced through the increase in deposition of atmospheric pollutants such as ammonia, that in their ionic form act as plant nutrients. The disproportionately high decline in the calcareous noda of species preferring high pH soils again implies that some changes in soil characteristics may have occurred.

## *4.5 Conclusions and further hypotheses*

The changes in relative abundance of species in some of the vegetation noda on Widdybank Fell have been investigated. Based on the ecological and physiological characteristics of the species and groups of species that have changed, various factors have been proposed as explanatory mechanisms. These include changes in the local climate resulting from the presence of Cow Green Reservoir or changes in the regional climate. Increased levels of deposition of atmospheric pollution acting as soil and plant acidifiers or nutrients may also have been responsible. Additionally, changes in the local management regime, for example in grazing intensity, may have been important. These factors are examined in detail in Chapters 5 and 6.

### *4.6 Summary*

- This chapter comprised investigations into the species that had significantly changed in abundance between the vegetation survey of Jones (1973) and the present vegetation survey.

- One of the most noticeable changes between the two vegetation surveys was the considerable loss of moss and liverwort diversity and of lichen abundance across the nine noda under study.

- More grasses, sedges and rushes had changed in abundance between the two vegetation surveys than would be expected by chance alone. Most of these had decreased in abundance.

- An examination was made of whether the species that had changed in abundance between surveys shared any particular physiological or ecological traits, compared to the flora of the nine noda as a whole. It was found that more stress-tolerators (as defined by Grime, 1977) had significantly decreased in abundance than would be expected by chance alone. The same was true for calcareous soil preferring species on the limestone grasslands.

- A number of factors that could be responsible for the observed changes in the vegetation were identified, including changes in the local climate (a potential effect of the construction of Cow Green Reservoir) or in the regional climate; changes in grazing intensity or in acid deposition. Future chapters will consider the potential importance of each of these factors.

# 5. Investigation of changes in the local climate produced by Cow Green Reservoir

## 5.1 Introduction

One of the potential effects of the construction of Cow Green Reservoir was a change in the local climate due to the thermal effects of the large body of water. Such a "lake effect" has been long documented elsewhere and results from the fact that it takes longer for water to adjust to any change in thermal input than it does for the land (Hulme & Barrow, 1997a). Consequently, in spring and early summer the water warms more slowly than the air and hence exerts a cooling influence upon the adjacent land. In late summer through to early winter the water is warmer than the air and re-emission of heat exerts a warming influence on the land. The Great Lakes of North America have been shown to raise mean January temperature by 2.8 °C and lower mean July temperature by 1.7 °C around their shorelines (Gregory & Smith, 1967). A local reduction in frosts and increase in air humidity is often also observed (Crowe, 1971). The occurrence and magnitude of lake effects vary greatly, depending on factors such as regional topography, the area of the water body, its depth, and the activity and direction of the general atmospheric circulation (Crowe, 1971).

Most documented cases of lake effects are for much larger water bodies than Cow Green reservoir, which has an area of 3.1 $km^2$ and a maximum water depth of 22.9 m. However Gregory & Smith (1967) carried out a study of Selset reservoir situated c. 13 km south-east of Widdybank (See Figure 1.1). Selset is of a comparable elevation (305 m a.s.l.) and area (1.1 $km^2$) to Cow Green. Over a two month period, August to early October 1965, two Stevenson screens were positioned near the reservoir, one on the north and one on the south shore. During periods of northerly or southerly winds, the difference between leeward and windward temperatures was small, <0.6 °C over 43 % of the time, with a maximum difference of 2.8 °C. The windward site was more often cooler than the leeward site i.e. at this time of year the water body was acting to cool the air mass. Widdybank Fell lies on the eastern shores of Cow Green Reservoir so could expect to receive the maximum impact of any "lake effect" as the prevailing wind comes across the reservoir from the south-west.

Harding (1979) compared climate data from Moor House and Widdybank Fell for the periods 1968-1970 and 1968-1977; before and after reservoir construction, respectively. He found a moderation of the lowest monthly screen minimum and grass minimum temperatures at Widdybank following reservoir construction. He also noted an annual reduction in the number of ground frosts. This study examined only a limited number of climate variables however, and did not investigate any seasonal effects of the reservoir upon the local climate.

The work described in this chapter tests the null hypothesis that the reservoir has had no effect on the local climate using meteorological data from Widdybank Fell and the nearby Moor House. In addition, a transect of dataloggers across the fell examined the spatial component of any "lake effect". Finally, data from relevés close to the reservoir margin were compared with those collected further away in order to determine if distance from the reservoir affected vegetation composition.

## 5.2 Methods

### *5.2.1 Comparison of climate data between Widdybank Fell and Moor House*

The meteorological instruments on Widdybank Fell are situated in an enclosure c. 225 m from the reservoir margin (513 m above sea level) on the west slope of the fell (G. R. NY 818 298). Daily meteorological observations were made manually at Widdybank from January 1968 to November 1995 inclusive. The reservoir was first filled in the spring of 1971. Hence the meteorological record prior to this was too short to permit a direct comparison of the climate at Widdybank before and after reservoir construction. This is because interannual variation over such a short period would mask the relatively subtle changes that might be produced by the reservoir. Hence the Widdybank meteorological record was compared with the record from Moor House. This station (G. R. NY758328) lies 5.7 km north-west of the Widdybank meteorological station (see Figure 1.1).

The Moor House station is at a higher elevation than Widdybank (560 m) and lies in an unimpounded catchment. Manual records for Moor House were taken from 1952 to 1979. The period 1968-1979 was thus common to both the Moor House and Widdybank record and could be used for comparison. Use of the Moor House record also allowed the separation of local climatic effects (of the reservoir) from any changes in the regional climate. Both sites currently have automatic weather stations, with records from 1996 at Widdybank and 1991 at Moor House. The record from Widdybank is fragmented, however, so these more recent records were not used in the present investigation. It had also been intended to use the Durham Observatory record as a further basis for comparison, but preliminary studies made it clear that the Durham climate was dissimilar (probably due to the influence of the sea) and so meaningful comparisons were not possible.

For all comparative analyses the meteorological records from both Widdybank and Moor House were first examined for any days with missing data for any of the recorded climate variables. Any missing entries for one site had the corresponding entry at the other site removed. Following construction of the reservoir dam, water level measurements were recorded for the filling reservoir. The mean water level and its standard deviation was calculated for the period 1970-1997. The water level of the reservoir first exceeded the lower 95 % confidence limit for the mean during the week 20-27th November 1970. This week was used as an appropriate cut-off period for the climate records into "pre-" and "post-" reservoir influence. Records from January 1968 to December 1973 were then used to provide a c. 3 year record pre- and post- reservoir construction. Several climate variables were examined at Widdybank and Moor House (Table 5.1). Unfortunately relative humidity could not be used. Relative humidity at Widdybank was calculated from wet and dry bulb temperatures. These data proved unreliable: calculations from these temperatures frequently produced a relative humidity that exceeded 100 %.

**Table 5.1 The climate variables that were examined using meteorological data from Widdybank Fell and Moor House. All were recorded daily at 0900 GMT.**

| Daily climate variable | Unit | Notes |
|---|---|---|
| Maximum temperature<br>Minimum temperature<br>Mean temperature<br>Temperature range | °C<br>°C<br>°C<br>°C | Maximum and minimum air temperatures were recorded in a Stevenson screen with the thermometer bulbs at 1.25 m above the ground (Meteorological Office, 1982). Daily mean is the mean of the maximum and minimum daily readings. Daily temperature range is calculated as the daily maximum minus the daily minimum temperature. |
| Grass minimum temperature | °C | This is recorded using a thermometer lying at least 2° to the horizontal over clipped grass with the bulb slightly lower than the stem. The bulb is at a height of 2.5-5 cm from the ground such that it is in contact with the tips of the grass (Meteorological Office, 1982). |
| Soil temperature at 30 cm depth | °C | The thermometer is suspended in a steel tube and buried under a grass surface. (Meteorological Office, 1982). |
| Total precipitation | mm | Collected in a rain gauge. |
| "Snow lying" | presence /absence | As depth of snow lying can be very variable locally (e.g. due to the effects of drifting) presence/ absence at 0900 GMT was used as a more comparable measure. |

Monthly means of each daily variable were taken for the period 1968-1973. For snow cover, instead of the mean, counts of numbers of days per month with snow lying were made. Monthly totals were used for precipitation. Differences in monthly means between Widdybank and Moor House were then calculated for the periods January 1968 to November 1970 inclusive ("pre-reservoir") and December 1970 to December 1973 ("post-reservoir"). The differences in monthly means between the two sites were compared for pre- and post- reservoir periods using single factor ANOVA.

An investigation was then carried out to determine if the differences between sites was related to the overall prevailing temperature. Based on the results from the previous analysis (see below), this was only carried out for grass minimum temperature. The difference in daily mean grass minimum temperatures (Widdybank Fell minus Moor House) was regressed upon the grass minimum temperature at Moor House (i.e. the prevailing, non-reservoir effect temperature). The first regression was carried out using the pre-reservoir daily data from the two sites (1st January 1968 to 23rd November 1970) and the second using the remaining data (24th November 1970 to 31st December 1973).

The influence of a water body upon the land can change according to season. Hence the climate data were examined for differences between Widdybank Fell and Moor House at a weekly resolution. All the previously examined climate variables were re-assessed. Additionally, the number of days per week with air frost (i.e. screen minimum air temperature fell to 0 °C or below) and ground frost (grass minimum temperature fell to 0 °C or below) were included. For this analysis 1968 was used as the "pre-reservoir" year rather than the mean of 1968-1970 (NB the reservoir first filled at the end of 1970 so this would have been an incomplete year). Climate data from 1971-1979 were used for the "post-reservoir" comparison and all post-reservoir years were expressed as anomalies with respect to 1968, as follows:

For each climate variable (e.g. weekly mean grass minimum temperature) four initial calculations were made:

1. For 1971 at Widdybank each weekly average grass minimum temperature had the weekly average grass minimum temperature for the corresponding week in 1968 subtracted from it, to produce a weekly anomaly. In the same way each week of 1972 had the corresponding value for 1968 subtracted from it. This was continued for the remaining years 1973-1979. Exactly the same procedure was carried out using the data from Moor House (1968 & 1971-1979) i.e. anomalies with respect to 1968 at Moor House were calculated.

2. The average of these weekly anomalies with respect to 1968 was then calculated for the entire period (1971-1979) for Widdybank and Moor House respectively. Finally, the difference in average weekly anomalies between stations was calculated (Widdybank minus Moor House).
3. It was likely that there would be *a priori* differences in the 1968 values for each week between Widdybank and Moor House. These weekly differences were calculated (Widdybank minus Moor House).
4. The mean difference for all 52 weeks between stations for 1968 was then calculated.

In order to correct for *a priori* differences in the 1968 values between the two stations, the final calculation for each week was as follows:

| | | | | |
|---|---|---|---|---|
| the 9 year mean anomaly between stations, Widdybank minus Moor House (i.e. calculation 2) | + | the weekly difference between Widdybank and Moor House in 1968 (i.e. calculation 3) | - | the 52-week mean difference between Widdybank and Moor House in 1968 (i.e. calculation 4) |

The resulting weekly mean anomalies were plotted as bar charts (see Results).

In order to test the significance of the differences for each week, the values in calculation 1 above were used i.e. the weekly anomalies with respect to 1968 for the years 1971-1979 from both stations. In this case, the corrections for possible *a priori* differences in the 1968 values between sites were carried out just on the Widdybank data (if calculated for both sites the effect would "cancel out") and for each year (1971-1979) separately.

e.g.

| | | | | |
|---|---|---|---|---|
| Widdybank week 1, 1971 minus week 1 1968 | + | the weekly difference between Widdybank and Moor House in 1968 for week 1 | - | 52 week mean difference between Widdybank and Moor House in 1968 |

Paired t-tests were carried out for each week comparing the nine years at Widdybank with the nine years at Moor House. Significance was tested using multiple probability (Wigley, Jones & Briffa, 1987). This calculates a new P value taking into account the number of tests performed using the formula:

$$P = 1 - (1 - p)^m$$

Where $p$ is the calculated probability value for the individual test and $m$ is the number of tests performed. In this case, for the 52 tests performed the equivalent of $P \leq 0.05$ for a single test is modified to $P \leq 0.001$ (approximately) for each test.

The calculations for the number of days with snow lying, or with air frost or ground frost were carried out slightly differently. Only calculations 1 and 2 above were used (not 3 or 4) to produce the bar charts. This was because a number of weeks in the year had no snow or frost, so the 52 week mean (calculation 4) would have been potentially inaccurate (this could have resulted in "false positives or negatives" in the overall calculation). Calculation 3 was not carried out because in the absence of calculation 4 it becomes redundant (weekly differences between Widdybank and Moor House in 1968 have already been taken into account in calculation 1). Rather than a paired t-test, a signs test (Sokal & Rohlf, 1969) was used to compare differences between stations (using the data from calculation 1). A signs test was more appropriate here because the counts of presence or absence made the data binomially distributed. The data were analysed in four week blocks in order to provide a sufficient number of comparisons.

Finally, two measures of the potential effects of any local climate change on plant growth were made. The first of these was a calculation of the length of the growing season. The growing season for most plant species is considered to span the period when daily mean temperature exceeds 5.5 °C (Manley, 1968). Upland plants can probably begin growth at lower temperatures, but this convention was retained. Growing season length was calculated using monthly mean data with a fitted line for the 5.5 °C cut-off period. The monthly mean screen temperature was compared to that at Moor House for pre- and post-reservoir periods (1969-1970 and 1971-1973, respectively).

Another measure considered to be of importance for plant growth is "growing degree days". This is calculated as the total number of degrees above 5.5 °C in the daily mean, accumulated across the whole year (Raper *et al.*, 1997). This was calculated using the same pre- and post- reservoir periods as used for the calculation of growing season above.

### *5.2.2 Investigation of differences in grass minimum temperatures at Widdybank Fell with distance from the reservoir*

In order to examine the difference in the "lake effect" with distance from the reservoir a calibrated pair of "Tinytag" dataloggers (Gemini Data Loggers Ltd, Chichester, UK) were positioned on Widdybank Fell. These were placed in short grass at c. 12 m (G. R. NY815297) and c. 310 m (G. R NY818299) from the reservoir edge (See overlay to vegetation map Sheet 3a). The loggers recorded daily grass minimum temperature from 5th February to 4th August 1998.

### *5.2.3 Differences in vegetation composition with distance from the reservoir*

This section describes an investigation into differences in the vegetation of Widdybank Fell with distance from Cow Green Reservoir. The relevés from the present vegetation survey were separated into two groups according to their distance from the reservoir. A distance of 382.5 m, determined by map measurement, was used to separate the relevés into one group close to the reservoir margin and one distant from the reservoir margin. This distance was selected as providing the most equal groupings for all the noda, although it was somewhat unsatisfactory for noda 3, 5 and 6 because the relevés were less well spread across the fell. Table 5.2 shows the division into the two groups of relevés. The frequency and median Domin score for each species in the two groups was calculated. CANOCO and Mann-Whitney U-tests were carried out comparing relevé data between the two groups in each nodum. An alternative method of comparison would have been to correlate abundance of each species in each nodum with distance from the reservoir. Although a more refined test for individual species, the disadvantage of this correlation method would have been its lack of direct comparability between noda.

**Table 5.2 The two groups of relevés from the present survey divided according to distance from the reservoir margin. These are listed in ascending order of distance from the reservoir margin.**

| Nodum | Numbers of relevés close to the reservoir margin | Mean distance from margin (m) with standard error in brackets | Numbers of relevés far from the reservoir margin | Mean distance from margin (m) with standard error in brackets |
|---|---|---|---|---|
| 1 | 800, 801, 802, 804, 803, 348 | 205 (70) | 516, 310, 308, 309, 805 | 569 (40) |
| 2 | 806, 808, 807, 809, 341 | 158 (82) | 343, 344, 347, 307, 518 | 496 (36) |
| 3 | 810, 813, 811, 814, 118, 335, 107 | 131 (51) | 812, 815, 816 | 992 (217) |
| 4 | 316, 319, 317, 325, 116, 110, 339 | 184 (42) | 103, 105, 102, 97, 80 | 490 (56) |
| 5 | 322, 817, 115, 315, 329, 134, 138, 313, 312, 113, 122, 120, 137, 818 | 180 (25) | 306 98 | 565 (15) |
| 6 | 327, 328, 333, 311, 324, 332, 336, 334, 337, 108 | 190 (22) | 96, 99, 508 | 555 (27) |
| 7 | 819, 119, 112, 117, 106 | 189 (58) | 94, 81, 13, 65, 63 | 634 (108) |
| 21 | 823, 820, 127, 504, 121, 137 | 190 (45) | 822, 826, 821, 824, 825 | 876 (97) |
| 33 | 828, 827, 829, 830, 831 | 126 (35) | 833, 832, 357, 358, 360 | 1241 (231) |

## 5.3 Results

### *5.3.1 Climate data*

Table 5.3 gives the results from the single factor ANOVAs comparing monthly means of daily climate variables for pre- (January 1968 to November 1970) and post-reservoir data (December 1970 to December 1973). The only climate variable for which there was a significant difference in pre-and post-reservoir data was grass minimum temperature. This is illustrated in Figure 5.1 with reservoir water-level data inset for comparison.

Figures 5.2 and 5.3 show the pre- and post- reservoir regressions for grass minimum temperature, respectively (Figures 5.1-5.3 redrawn after Figure 2 in Huntley *et al.*, 1998). Prevailing temperature was related to the difference in grass minimum temperature between sites for both time periods (Table 5.4). However the regression for the pre-reservoir period had a small $R^2$ with an intercept not significantly different from zero and a small slope. In contrast, the regression for the post-reservoir period had a much larger $R^2$ with an intercept significantly different from zero and a larger slope. The slopes of the two lines were also significantly different ($t=8.69$, d. f. 2168, $P \leq 0.001$). The difference between the regressions for the pre- and post- reservoir periods clearly illustrates the effect of the presence of the reservoir at Widdybank. Examining the regression for the post-reservoir period it can be seen that when the prevailing temperature is at its coldest (i.e. grass minimum temperature at Moor House is very low) the effect of the reservoir in warming grass minimum temperatures at Widdybank is greatest. This difference can be up to 10 °C between sites on the coldest nights.

**Table 5.3 Results from single factor ANOVA comparing differences between Widdybank Fell and Moor House in terms of monthly means of daily variables before and after reservoir construction. Degrees of freedom 1, 70 for all tests.**

| Daily variable | F value | P value |
|---|---|---|
| Maximum temperature (°C) | 0.62 | 0.43 |
| Minimum temperature (°C) | 1.54 | 0.22 |
| Mean temperature (°C) | 1.42 | 0.24 |
| Temperature range (°C) | 0.52 | 0.47 |
| Grass minimum temperature (°C) | 55.30 | $1.96 \times 10^{-6}$ |
| Soil temperature at 30 cm depth (°C) | 0.51 | 0.48 |
| Precipitation (mm) | 0.83 | 0.37 |
| Number of days with snow lying | 1.48 | 0.23 |

**Table 5.4 The difference in monthly mean grass minimum temperature (Widdybank Fell minus Moor House) regressed upon grass minimum temperature at Moor House for pre- and post- reservoir periods.**

| | Regression for pre-reservoir period (1/1/68 - 23/11/70) | Regression for post-reservoir period (24/11/70 - 31/12/73) |
|---|---|---|
| $R^2$ | 0.01 | 0.15 |
| Gradient | -0.03 | -0.16 |
| Standard error of gradient | $9.4 \times 10^{-3}$ | 0.01 |
| y intercept | -0.03 | 0.93 |
| F | 10.07 | 191.85 |
| P | $1.6 \times 10^{-3}$ | $2.2 \times 10^{-40}$ |
| Degrees of freedom | 1, 1049 | 1, 1117 |
| Significance of intercept from zero | t=0.51, P=0.61 | t=15.57, P=$1.2 \times 10^{-49}$ |

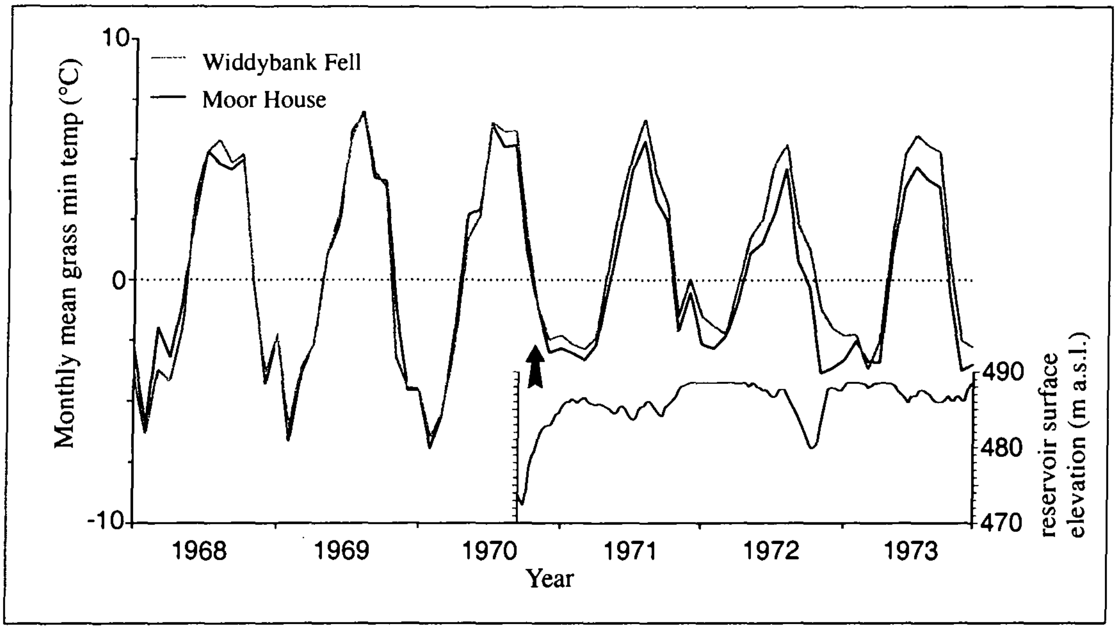



**Figure 5.1 Monthly means of daily grass minimum temperature compared between Widdybank Fell and Moor House for the c. 3 years before and after reservoir filling. Inset graph shows the water level of the reservoir; the arrow indicates the division into pre- and post- reservoir records for ANOVA.**

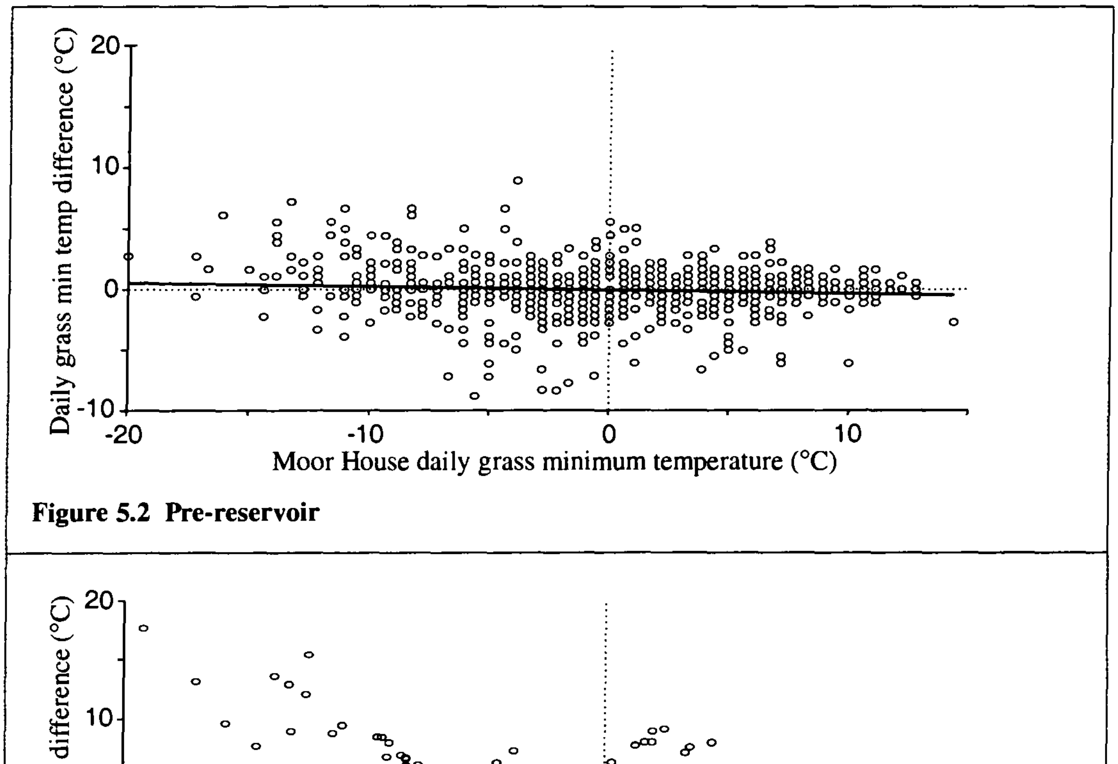



**Figure 5.2 Pre-reservoir**

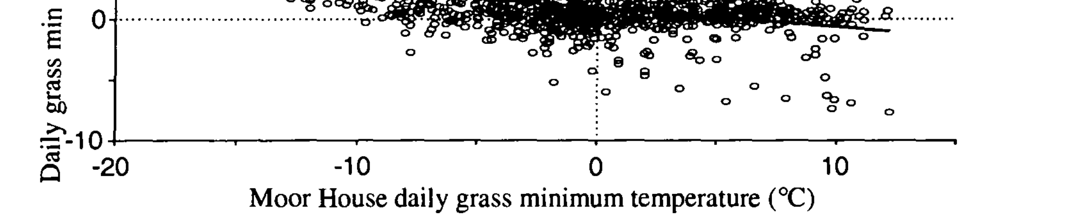



**Figure 5.3 Post-reservoir**

**Figures 5.2 & 5.3 Regressions of the daily grass minimum temperature difference (Widdybank Fell minus Moor House) against the daily grass minimum temperature at Moor House for pre- and post- reservoir periods, respectively.**

Figures 5.4-5.13 show the results from weekly analysis of the difference between Widdybank Fell and Moor House with respect to "pre-reservoir" year 1968 for a selection of climate variables. (Figures 5.6 & 5.8 redrawn after Figure 3 in Huntley *et al.*, 1998). The trend apparent in the variables recorded at screen height (maximum, minimum and mean, Figures 5.4-5.6) is for a cooler late winter/spring and warmer late summer/autumn at Widdybank compared to Moor House since reservoir construction (in the anomaly with respect to 1968). The magnitude of this change in the mean is c. 0.25 °C.

The temperature range between stations (in the anomaly with respect to 1968) (Figure 5.7) has increased slightly in spring and decreased slightly in autumn. The difference in precipitation between stations in the anomaly is up to 1 mm per week in summer (Figure 5.10). Weeks 9-12 (early spring) and 45-48 (early winter) at Widdybank receive significantly fewer air frosts compared to Moor House (Figure 5.11). The greatest observed differences, however, were in the boundary-layer variables. There has been an all year round increase in the grass minimum temperature at Widdybank compared to Moor House (in the anomaly with respect to 1968) by c. 1°C (Figure 5.8) but the greatest difference between stations occurs in autumn. This translates to a reduction in the number of ground frosts at Widdybank in the anomaly by up to one day a week, particularly during the second half of the year (Figure 5.12). The number of days per week with snow lying at Widdybank has also decreased (Figure 5.13). Soil temperatures at this station in the winter months are c. 0.25 °C warmer in the anomaly with respect to 1968 than at Moor House (Figure 5.9).

**Figures 5.4-5.10 Weekly mean differences (Widdybank Fell minus Moor House) for the period 1971-1979 with respect to 1968 for a selection of climate variables. Shading of the bars indicates the level of significance between stations in a paired t-test: unfilled P≤0.05, grey P≤0.05, black P≤0.05 at the multiple probability level.**

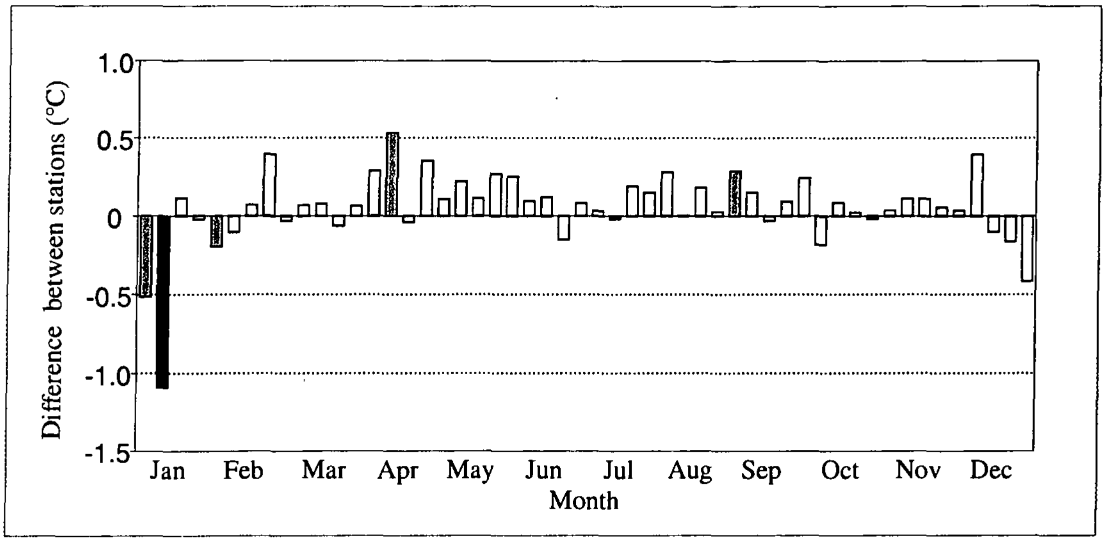



**Figure 5.4 Weekly mean daily maximum screen temperature difference (in the anomaly with respect to 1968) between stations.**

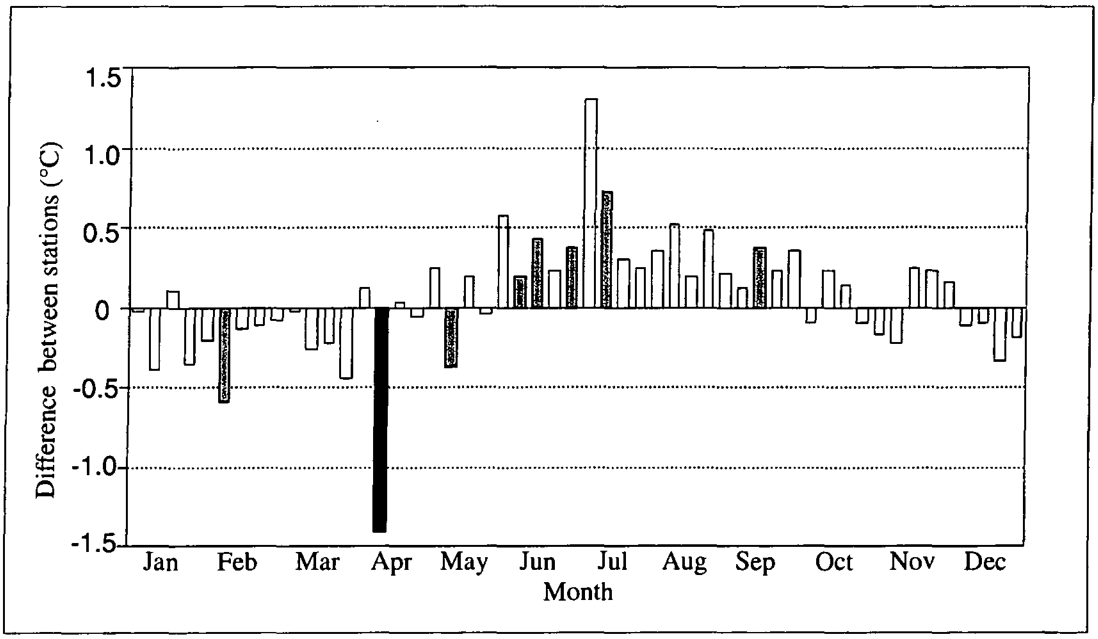



**Figure 5.5 Weekly mean daily minimum screen temperature difference (in the anomaly with respect to 1968) between stations.**

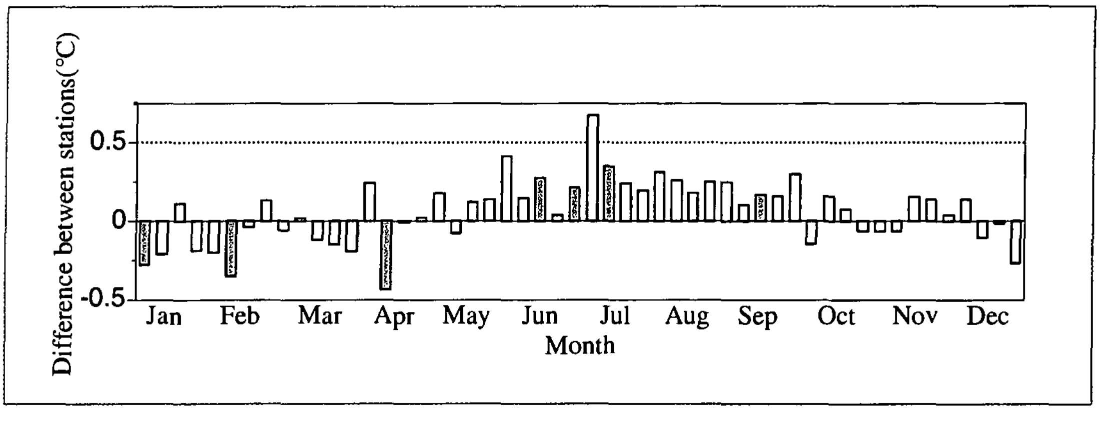



**Figure 5.6 Weekly mean daily mean screen temperature difference (in the anomaly with respect to 1968) between stations.**

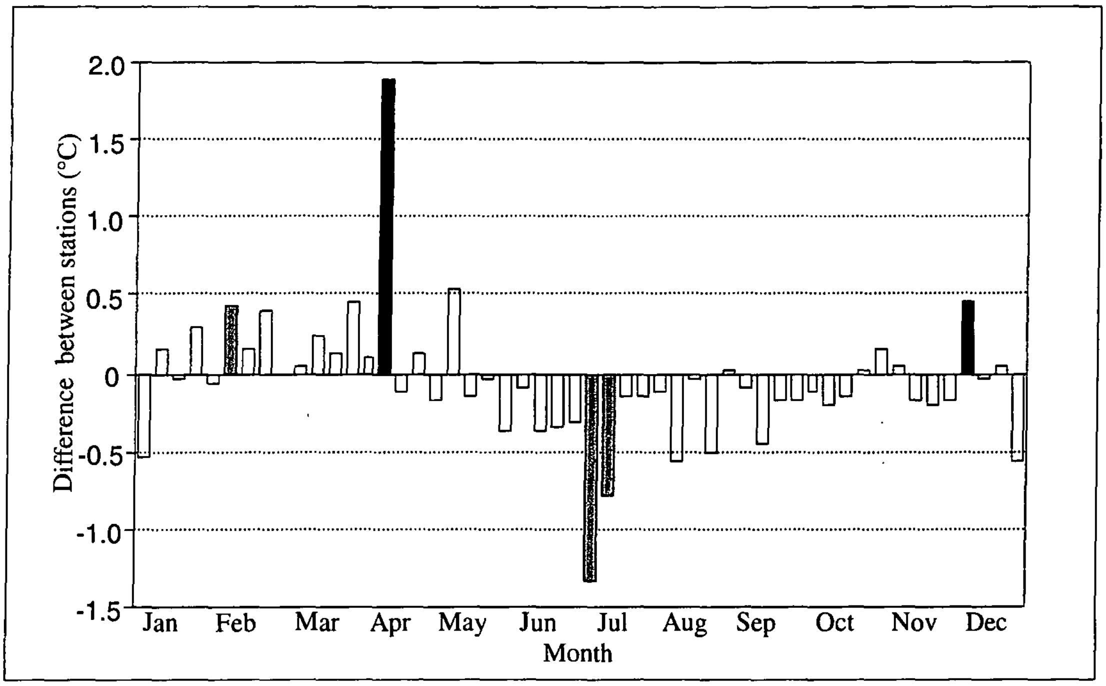



**Figure 5.7 Weekly mean daily screen temperature range difference (in the anomaly with respect to 1968) between stations.**

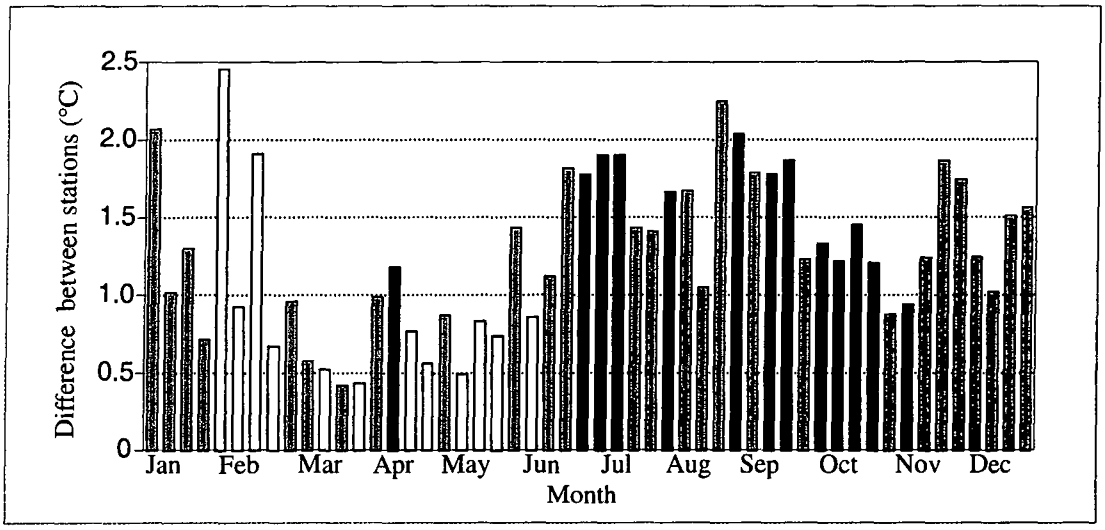



**Figure 5.8 Weekly mean daily grass minimum temperature difference (in the anomaly with respect to 1968) between stations.**

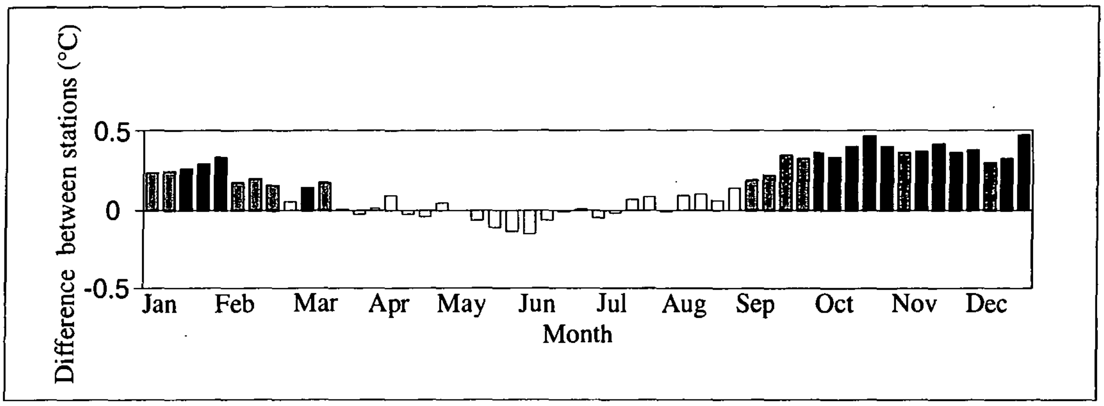



**Figure 5.9 Weekly mean daily soil temperature (depth 30 cm) difference (in the anomaly with respect to 1968) between stations.**

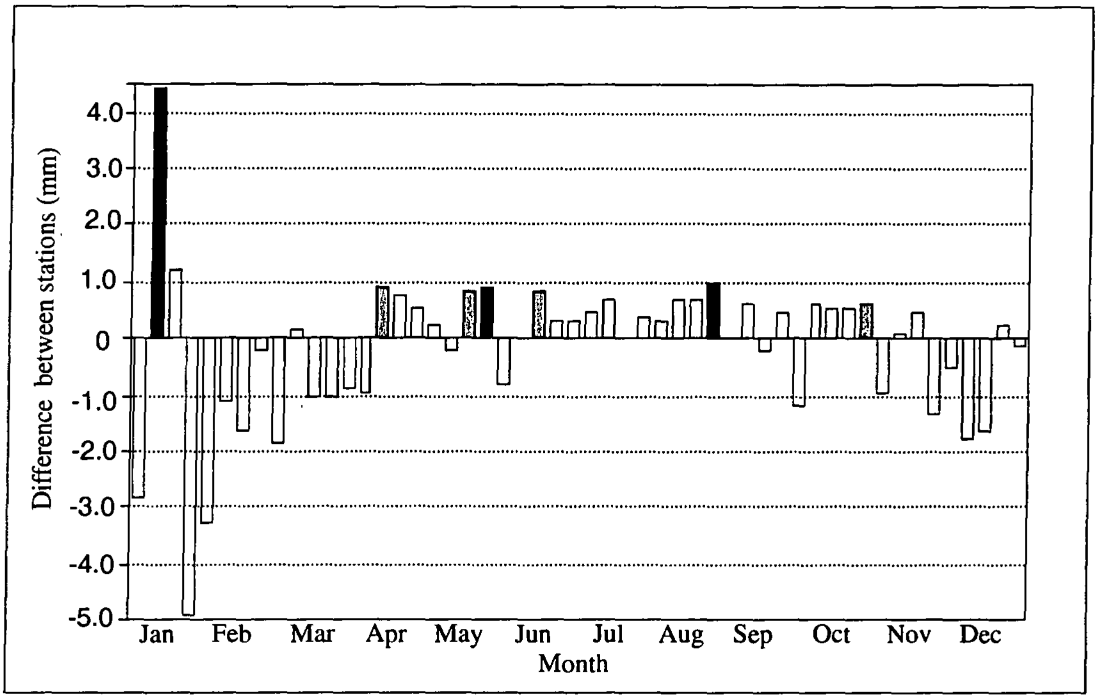



**Figure 5.10 Weekly mean daily precipitation difference (in the anomaly with respect to 1968) between stations.**

**Figures 5.11-5.13 Weekly mean difference (Widdybank Fell minus Moor House) for the period 1971-1979 with respect to 1968 for a selection of climate variables. Groups of four weeks (each bar below is the mean of a four week group) were tested for significance between stations using a signs test: unfilled bars P≤0.05, grey P≤0.05, black P≤0.01.**

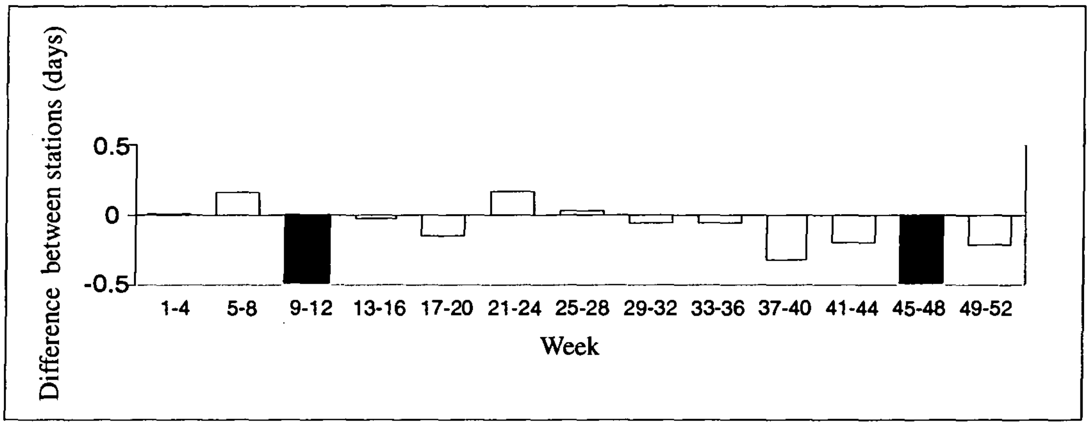



**Figure 5.11 Mean number of days per week with air frost; difference (in the anomaly with respect to 1968) between stations.**

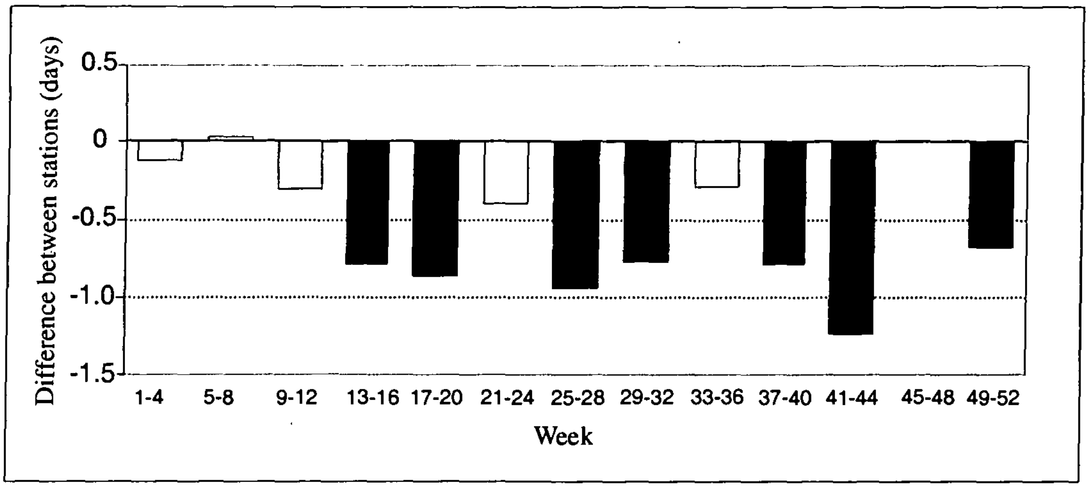



**Figure 5.12 Mean number of days per week with ground frost; difference (in the anomaly with respect to 1968) between stations.**

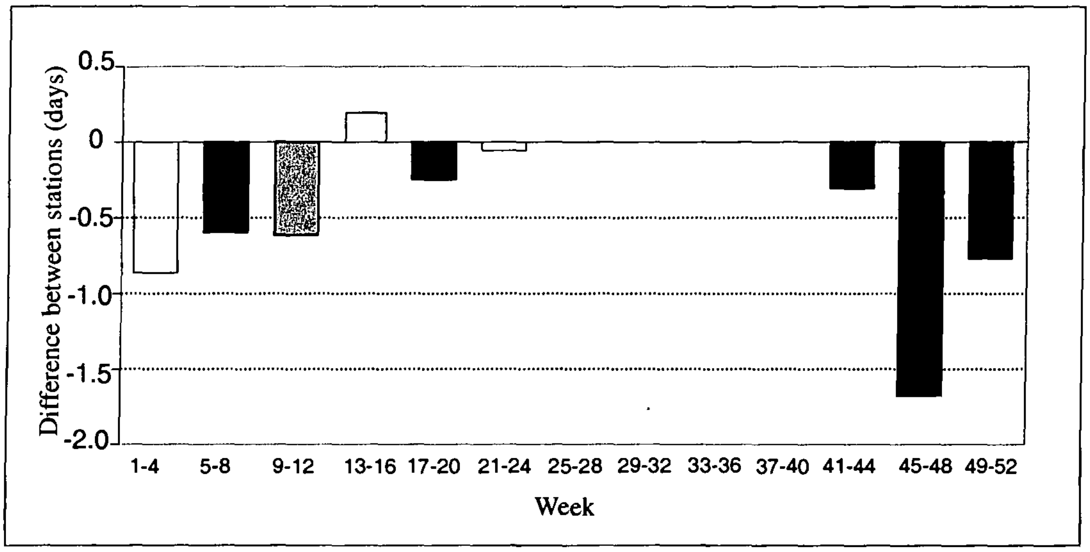



**Figure 5.13 Mean number of days per week with snow lying; difference (in the anomaly with respect to 1968) between stations.**

There was no discernible difference in the length of the growing season between Widdybank and Moor House for pre- (1969-1970) and post- (1971-1973) reservoir periods (Figures 5.14 & 5.15). At Widdybank, the growing season for both periods is from mid-April to mid-October. It is slightly shorter at Moor House (later by around a week in spring) because of the increased altitude at this site. Additionally, Widdybank had an average of 158 more growing degree days than Moor House over the period 1968-1970. Over the post reservoir period 1971-1973 this averaged 237, but the difference between the two periods was not significant.

### *5.3.2 Differences in grass minimum temperature with distance from the reservoir*

There was a significant difference in grass minimum temperature between the two dataloggers on Widdybank Fell ($F=8.69$, d. f. 1, 360, $P=0.003$). Figure 5.16 shows that the grass minimum temperature close to the reservoir was consistently warmer throughout the recording period. The mean difference between the two loggers was 1.4 °C. During the coldest periods however, the grass minimum temperature by the reservoir was warmer by up to c. 5° C.

### *5.3.3 Vegetation data*

Only five species were significantly different in abundance between the two relevé groups in any nodum. These were *Minuartia verna* and *Racomitrium lanuginosum* in Nodum 2, *Agrostis vinealis* in Nodum 4, *Antennaria dioica* in Nodum 5 and *Ranunculus acris* in Nodum 21 (see Table 5.5 below). There was no significant difference for any species between the two relevé groups in the other four noda. Out of the total of 604 individual Mann-Whitney tests performed across the nine noda, 30 could be expected to be significant where $P \leq 0.05$ by chance alone. Hence these five significant results can be given little weight. The results from CANOCO were also not significant in any nodum. Critical values of U where $P \leq 0.05$ were 23 (Nodum 2), 30 (Nodum 4), 27 (Nodum 5) and 27 (Nodum 21). Numbers of quadrats in each test are given in Table 5.2 above.

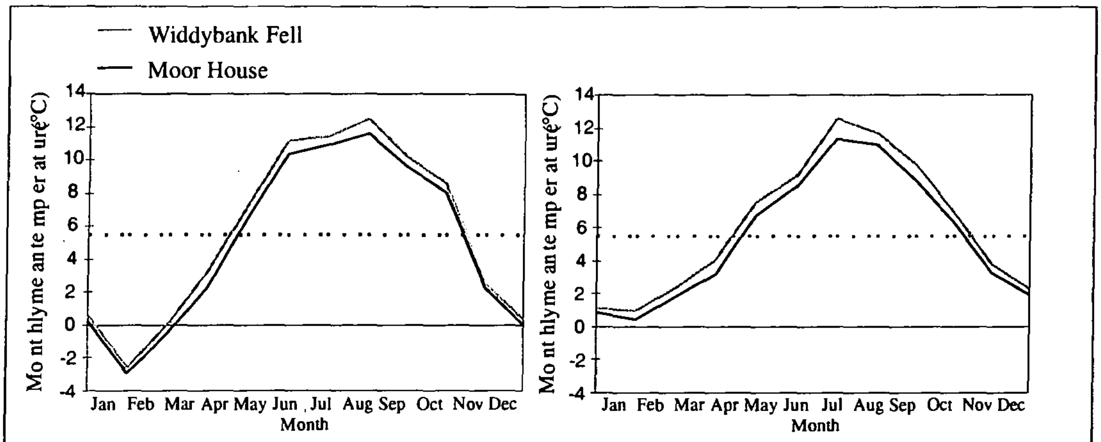



**Figure 5.14 Pre-reservoir (1969-1970)** **Figure 5.15 post-reservoir (1971-1973)**

**Figures 5.14 & 5.15 Length of the growing season at Widdybank Fell and Moor House for pre- and post- reservoir periods, respectively. Each graph shows the monthly mean screen temperature for the respective 3 year period, with a fitted line at 5.5 °C. (This is the temperature above which the "growing season" is conventionally considered to occur (Manley, 1968)).**

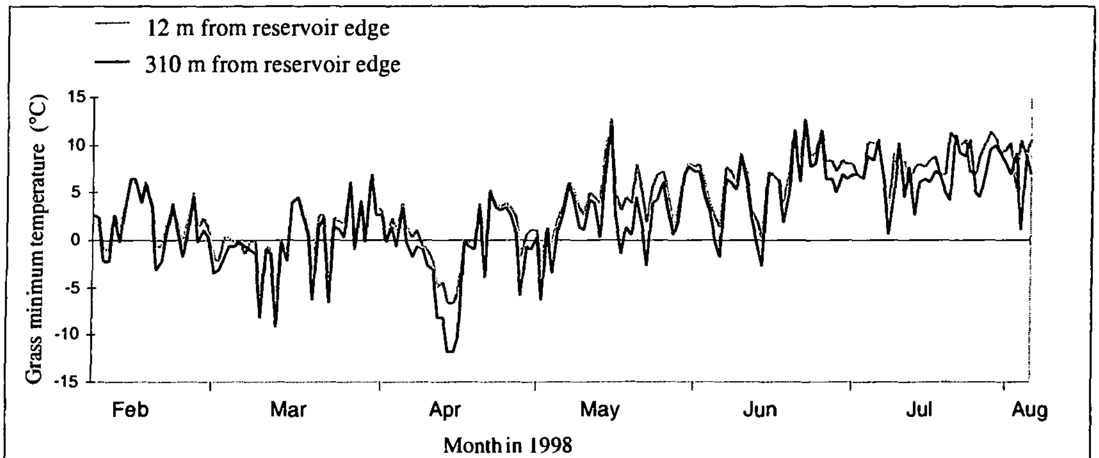



**Figure 5.16 Daily grass minimum temperature recorded from two dataloggers on Widdybank Fell from 5/2/98 to 4/8/98. One logger was positioned close to (c. 12 m) the reservoir edge, the other was further away (c. 310 m).**

**Table 5.5 The five species that were significantly different in abundance according to distance from the reservoir. Frequency of occurrence (F) and median Domin score (D) are given for both groups as well as the values of U in the Mann-Whitney test.**

| | **Nodum in which significant difference** | **Near to reservoir** | | **Far from reservoir** | | **value of U** | **Species more or less abundant close to the reservoir?** |
|---|---|---|---|---|---|---|---|
| | | F | D | F | D | | |
| *Agrostis vinealis* | 4 | 0.14 | 3 | 1.00 | 3 | 32.0 | less |
| *Antennaria dioica* | 5 | 0.07 | 1 | 1.00 | 3 | 28.0 | less |
| *Minuartia verna* | 2 | 0.60 | 1 | 1.00 | 2 | 23.5 | less |
| *Racomitrium lanuginosum* | 2 | 1.00 | 2 | 0.60 | 1 | 23.5 | more |
| *Ranunculus acris* | 21 | 0.20 | 2 | | | 27.5 | more |

## *5.4 Discussion*

It would be expected that the climate variables recorded in the boundary layer between the earth and the air would be most modified by any "lake effect". This is because the earth is a better conductor of heat; ground frosts occur more frequently than air frosts, for example (Barrow & Hulme, 1997). Hence it is not surprising that at Widdybank Fell there was a significant difference in monthly mean grass minimum temperatures between the three year pre- and post-reservoir periods compared to Moor House. It might have been expected that the number of days with snow lying would also have been affected. Snow is clearly a seasonal phenomenon however, so for much of the year there would be no difference in snow cover between sites (because snow would be absent entirely). Any changes in snow cover could thus be better observed at a weekly resolution.

The results from the grass minimum temperature regression show that moderation of temperature by the reservoir appears to occur during periods of climatic extremes, especially of cold. Thus it was interesting to find out whether there were periods during the year when the reservoir might have a significant local climatic effect even though there was no overall effect at a coarser temporal resolution.

Investigation of mean weekly differences between Widdybank Fell and Moor House in the anomaly relative to 1968 illustrated the clear seasonal effects of Cow Green Reservoir upon the local climate at Widdybank. As demonstrated from the analyses above, the strongest effects were seen in the boundary layer, with an all year round moderation of grass minimum temperatures and reduction in number of ground frosts. It is interesting that the screen mean was slightly cooler in spring and warmer in autumn. These changes in minimum and mean temperatures both correspond to the classic "lake effect" described in the introduction. It would not generally be expected that precipitation would be affected by such a relatively small body of water (e.g. Crowe, 1971) so the observed increase in precipitation at Widdybank was somewhat surprising.

The evidence from the dataloggers on Widdybank Fell of a significant moderation of grass minimum temperatures close to the reservoir margin is as would be expected. Ideally, a network of loggers recording a number of climate variables could have been established on the fell to fully model the extent of the influence of the "lake effect". Unfortunately constraints on the number of dataloggers available and equipment failure meant that this was not possible.

It is not surprising that there was no difference in the length of growing season after reservoir construction, given the lack of overall difference in monthly mean screen temperatures over this period as previously calculated (Table 5.3). Examination of the 1971-1979 weekly record indicated a 0.25 °C reduction in screen mean temperature in spring and an increase by the same amount in autumn (Figure 5.6). Such a change would probably not be discernible in affecting the length of the growing season. Even if it did have some effect, perhaps by making the growing season a day later in spring, this would be compensated for by a corresponding extension of the season in autumn, so the overall length would not have changed. There was also no significant difference in the number of growing degree days pre- and post- reservoir construction. Using conventional methods of assessing climate therefore, based on mean temperatures, the potential effects of the reservoir on plants, particularly through the moderation of minima, could be missed.

It is clear that the reservoir has exerted an influence on the local climate of Widdybank Fell, hence the null hypothesis is rejected. What would be the likely effects on the vegetation of such a climate change? Firstly, a note should be made of the significance of the magnitude of these changes. The Holocene (the c. 10000 year period since the last glacial) is considered to have been relatively stable climatically (Hulme & Barrow, 1997a). It is estimated that mean temperatures in the British Isles have not changed by more than 1 °C (Hulme & Barrow, 1997a). Hence a change of c. 0.25 °C in the mean (spring and autumn) and an increase in weekly grass minimum of c. 1 °C is clearly of significance, particularly since these were a step rather than a gradual change. It must also be remembered that plants are growing in the boundary layer, and changes in mean temperatures here will probably be greater than changes recorded at screen height. The United Kingdom Climate Change Impacts Review Group (1996) considered that a temperature change of >0.5 °C that lasted for more than ten years was of potential importance for ecosystems. This observed climate change produced by Cow Green Reservoir therefore clearly has the potential to be of significance for plant growth.

Cold temperatures, and particularly freezing stress, inhibit photosynthesis and $CO_2$ assimilation (Salisbury & Ross, 1992). For mountain plants night-time temperatures (i.e. minima) are of particular significance because of the limitations they put on developmental processes such as flower formation (Körner & Menendez-Riedl, 1989). Over an entire season therefore, the reduction of frosts and periods of extreme cold may lead to increased growth and faster development. This could be particularly noticeable for evergreen species, able to respond opportunistically to favourable winter temperatures. Additionally a reduction in "killing frosts" in late spring could be of importance for many species. Milder winter and a reduced likelihood of frosts during the growing season could facilitate the invasion of "lowland" species, either on a seasonal or permanent basis. A large propagule source is potentially provided via sheep fed on hay who may then transport the hayseed in their guts.

Growth responses to moderated temperatures in spring and autumn will partly depend on the factors that control breaking and resuming of dormancy (of seeds or perennating organs). For example, many alpine species can respond opportunistically to warmer spring temperatures in terms of beginning their growth, but leaf senescence in autumn is controlled by photoperiod rather than temperature (Körner, 1995).

Slightly warmer mean autumn temperatures, with a later incidence of hard frost, could aid successful seed-set in many species, and be of particular importance for annuals such as *Euphrasia rostkoviana* or biennials such as *Gentianella amarella*. Several of the "Teesdale rarities" are short-lived perennials, with no capability for vegetative reproduction, for example *Polygala amarella*, so could also benefit from more favourable autumn temperatures. A reduction in number of days with snow lying could, paradoxically, be harmful to some species. Snow cover provides considerable protective insulation for plants and if its persistence is reduced, sharp cold spells could be more damaging than if the plants were still covered.

The local climate change also has the potential for indirect effects on plants. For example, milder winters could produce an increase in survival of plant pests and pathogens, but equally more insect pollinators might survive. Another important effect could be on the rates of mineralisation of soil organic matter. Mineralisation is the release of inorganic nutrients from organic material via microbial activity. Temperatures in the uplands are generally sub-optimal for soil microbial activity (e.g. Harrison *et al.*, 1994) so it is possible that a moderation of minima may result in a net annual increase in soil mineralisation. In a strongly nutrient-limited system such as Widdybank, even a modest increase in rates of nutrient turnover or a change in the timing of nutrient "flushes" could be important for plant growth.

To summarise therefore, the modifications in mean and especially grass minimum temperatures produced by Cow Green Reservoir had the clear potential to be of significance for the local vegetation. The changes in the local climate could have resulted in changes in the relative competitive success of certain species and thus altered the composition of the plant communities on Widdybank Fell.

Given the considerable potential for the reservoir to have an effect on the vegetation, it is interesting that there was no difference in vegetation composition between the two groups of relévès separated according to distance from the reservoir. A similar survey by Maxwell (1997), (see Chapter 1) along a transect of Nodum 4 vegetation found statistically significant differences between only three species (out of 33 recorded in the nodum) related to distance from the reservoir. This lack of evidence for a spatial effect based on distance from the reservoir could imply that the presence of the reservoir has not been responsible for the observed vegetation changes. There is a clear need to examine other factors that may have been responsible for these changes. These are considered in Chapter 6.

## 5.5 Conclusions

The work described in this chapter has demonstrated significant local climate changes resulting from the presence of Cow Green Reservoir. Hence the null hypothesis that Cow Green Reservoir has had no effect on the local climate has been rejected. Principally there was an all year round moderation of minima at Widdybank Fell compared to Moor House (in the anomaly with respect to pre-reservoir year 1968). This was most apparent for boundary-layer variables such as grass minimum temperatures and days with snow lying. Additionally there was a slight reduction of mean temperatures in spring and a corresponding increase in mean temperatures in autumn at Widdybank, again in the anomaly with respect to

1968, compared to Moor House. Both these changes are consistent with those expected by the classic "lake effect". These observed changes in local climate had the potential to affect the relative competitive success between species and thus the composition of the vegetation of the fell. However, a comparison of relevés from the present vegetation survey showed no difference in species composition with distance from the reservoir margin. This is an unexpected result, given the considerable potential for vegetation change. Other factors that may be responsible for the observed changes in the vegetation are examined in Chapter 6.

### 5.6 Summary

- Opponents of the construction of Cow Green Reservoir hypothesised that it might modify the local climate, in terms of creating a "lake effect" with the potential for impacts on the local vegetation. Some examples of the "lake effect" are given, which typically include producing cooler mean temperatures in spring and warmer mean temperatures in autumn as well as the potential for a moderation of minima.

- Meteorological records from Widdybank Fell and the nearby Moor House were compared in order to test the null hypothesis that the presence of Cow Green Reservoir has not altered the local climate at Widdybank Fell. Differences between the two stations were compared with respect to "pre-reservoir" year 1968.

- There were significant differences between Widdybank Fell and Moor House (in the anomaly with respect to 1968) for a number of climate variables. An all year round reduction in grass minimum temperature by c. 1 °C at Widdybank compared to Moor House was observed. This was most pronounced when prevailing temperatures were at their coldest. The number of days with snow lying was also reduced at Widdybank. Screen mean temperatures were cooler by c. 0.25 °C in spring, and warmer by a similar amount in autumn. The null hypothesis of no effect of the reservoir on the local climate was hence rejected. These observations are consistent with those expected by the action of the classic "lake effect".

- A pair of dataloggers recording grass minimum temperature were situated c. 12 m and c. 310 m from the reservoir edge on Widdybank Fell. Grass minimum temperatures recorded by the logger at the reservoir edge were warmer by an average of 1.4 °C and by up to c. 5 °C over the 6 month recording period.

- Conventional measures of climate for plant growth (length of growing season and growing degree days) detected no change produced by the reservoir. These measures are however based on daily mean screen temperatures and the moderation of grass minima in particular could be of significance for plant growth.

- A comparison of present-day relevé data from quadrats close to and further from the reservoir margin, however failed to show any significant differences in the composition of the vegetation. This result was surprising, but emphasised the need to consider the effects of other environmental factors that may have changed in the period between the two vegetation surveys.

# 6. Investigation of changes in the regional climate and other environmental factors

## 6.1 Introduction

This chapter considers the potential influence of environmental factors on the vegetation that have not previously been discussed in Chapter 5. These include factors that are not related to the presence of the reservoir and may have changed since the vegetation survey of Jones (1973) namely:

- Changes in the management regime on Widdybank Fell - specifically changes in grazing intensity.
- Changes in the regional climate.
- Changes in concentration of atmospheric carbon dioxide.
- Changes in deposition of atmospheric pollutants such as inorganic sulphur and nitrogen compounds that may act as plant nutrients and/or soil acidifiers.

## 6.2 Grazing

The predominant management practice on Widdybank Fell is grazing by Swaledale sheep. The exact numbers of sheep on the fell in recent years cannot be determined. However numbers appear to have remained fairly constant since the 1960s, at approximately 500 (± 10) plus followers (i.e. lambs), with some annual variation as to timing of access to the fell (Alan Scott, the tenant farmer, *pers. comm.*). Highland cattle and fell ponies have also had grazing access for short periods between the dates of the two surveys.

The tenancy agreement with the farmer recently expired, and in 1997 the fell was left ungrazed. This coincided with one of the two years over which the present vegetation survey was carried out. However there was very little apparent difference in the vegetation between 1997 and the previous year, although more species succeeded in flowering. It is hence unlikely that this change in grazing pressure over one season could account for the observed changes in the vegetation between the two surveys. From 1998 onwards, stocking levels have been reduced to 200 ewes and 50 hogs (young sheep). The hogs are kept on the fell all year whereas the ewes are removed between April and the end of July. This change will almost certainly have some future impact and the vegetation will need to be monitored carefully.

Grazing by rabbits is also of some importance. It is however impossible to gain accurate records of rabbit numbers. Although they have been continually controlled since the 1970s, control takes the form of underground gassing so numbers killed are not known (Chris McCarty, English Nature site manager, *pers. comm.*). However the effects of rabbit activity are extremely localised. Only five quadrats in the entire vegetation survey showed evidence of intensive rabbit grazing. These were 823, 827, 810 and 806 on vegetation map Sheet 1 and 816 on vegetation map Sheet 5.

Other ways in which the vegetation may be disturbed is through burning and trampling. Some burning of heather occurs on the fell as part of the management for grouse (described in Chapter 2) but burning does not occur in the vegetation noda included in this study. Trampling pressure from tourists may be heavy (see Chapter 2) but this is localised to areas adjacent to the Birkdale track and thus will have affected a minimal number of quadrats.

## 6.3 Regional climate

### 6.3.1 Introduction

In addition to the modification of the local climate produced by Cow Green Reservoir, it was necessary to investigate whether the observed changes in the vegetation were the result of a larger-scale climate change. An investigation of changes in climate at Moor House over the period 1931-1995 was published recently (Garnett, Ineson & Adamson, 1997). The record used was derived from both manual and automatic weather station data from the site. The gap in the Moor House record from 1980-1990 was supplemented by data from Widdybank Fell (which had been corrected previously for any systematic differences between sites). From this combined record there was no evidence of a trend in monthly or annual mean air temperatures. The next section extends the investigation, by examining if there have been any changes in daily or annual temperature ranges. Changes in seasonality of rainfall are also discussed.

### *6.3.2 Changes in daily or annual temperature ranges*

Initially, the period for which records were available for both Widdybank and Moor House (1968-1979) were examined for any differences in daily temperature range (i.e. daily maximum minus daily minimum temperature). This was tested using a single-factor ANOVA comparing data from the two sites. There was no significant difference in daily temperature range between the two stations between 1968 and 1979 ($F=0.27$, d. f. 1, 8646; $P=0.60$).

In addition, to provide a longer-term analysis of the climate records the daily temperature range from 1952-1995 was then also calculated, using three data sets:

- The Moor House record, 1952-1967.
- The records from Widdybank and Moor House from 1968-1979 (from which a mean daily temperature range was calculated).
- The Widdybank record, 1980-1995.

The daily temperature range from 1952-1995 was regressed upon time. It has already been demonstrated, above, that there was no systematic difference in daily temperature range over the period of record overlap between the two sites (1968-1979). Hence in this case (compared with the study of Garnett *et al.*, 1997) no correction factor needed to be applied to account for the different sources of the climate data. The results of the regression using the combined datasets are in Table 6.1. Between 1952 and 1995 there has been a significant decrease in daily temperature range of 0.0165 °C per year. Hence over the entire 43 year period there has been a decrease in daily temperature range of 0.71 °C. Additionally, any change in annual temperature range was investigated over the same period (1952-1995) using the same combined dataset. Firstly the extreme temperature range (coldest daily minimum to warmest daily maximum) for each year was

**Table 6.1 Regression of daily temperature range upon time for 1952-1995 for the Moor House/Widdybank records.**

| | daily temperature range |
|---|---|
| $R^2$ | 0.04 |
| gradient | $4.5 \times 10^{-5}$ |
| y intercept | 7.41 |
| F | 57.35 |
| P | $3.8 \times 10^{-14}$ |
| degrees of freedom | 1, 15777 |

**Table 6.2 Regressions of annual temperature range upon time for 1952-1995 for the Moor House/Widdybank records.**

| | extreme annual range | monthly mean range |
|---|---|---|
| $R^2$ | 0.13 | 0.01 |
| gradient | -0.09 | 0.02 |
| y intercept | 41.93 | -17.31 |
| F | 6.30 | 0.45 |
| P | 0.02 | 0.51 |
| degrees of freedom | 1, 43 | 1, 43 |

**Table 6.3 Monthly mean daily temperature ranges regressed upon time for the Moor House/Widdybank record from 1952-1995.**

| | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sept | Oct | Nov | Dec |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $R^2$ | 0.05 | 0.03 | 0.10 | 0.05 | 0.04 | 0.04 | $6.9 \times 10^{-4}$ | $3.6 \times 10^{-4}$ | 0.04 | 0.12 | 0.06 | 0.22 |
| gradient | -0.01 | -0.04 | -0.03 | -0.02 | -0.02 | -0.02 | $3.0 \times 10^{-3}$ | $2.0 \times 10^{-2}$ | -0.02 | -0.02 | -0.01 | -0.03 |
| y intercept | 27.18 | 77.17 | 60.45 | 49.57 | 44.38 | 45.87 | 20.54 | 3.35 | 35.96 | 42.48 | 29.30 | 60.15 |
| F | 2.07 | 17.28 | 4.46 | 2.35 | 1.92 | 1.59 | 0.03 | 0.02 | 1.79 | 5.52 | 2.57 | 11.46 |
| P | 0.16 | $1.6 \times 10^{-4}$ | 0.04 | 0.13 | 0.17 | 0.21 | 0.09 | 0.90 | 0.19 | 0.02 | 0.12 | $1.5 \times 10^{-3}$ |
| degrees of freedom | 1, 41 | 1, 41 | 1, 41 | 1, 41 | 1, 42 | 1, 42 | 1, 42 | 1, 42 | 1, 42 | 1, 42 | 1, 42 | 1, 41 |

calculated. For the period 1968-1979, when records were available from both sites, the mean of the daily maximum and minimum from the two sites was taken. Secondly, the monthly mean range for each year was calculated (the month with the warmest mean temperature minus the month with the coldest mean temperature). Both of these measures of annual temperature range were regressed upon time for the period 1952-1995. The results of these regressions are given in Table 6.2. There has been a reduction in extreme annual temperature range by 3.97 °C over the 44 years covered by the record, but no significant change in mean annual range. In order to determine if the moderation in daily temperature ranges was consistent all year round, the mean daily temperature range for each month of the year was separately regressed upon time. There were significant differences over the period 1952-1995 for the months of February, March, October and December (Table 6.3). These tests were repeated for each month using just the period 1968-1979, but in no case were the results significant.

It might have been expected that an increase in long-term mean air temperatures would have been apparent from the Moor House and Widdybank combined record. There has been a rise in global mean surface air temperature of between 0.3 and 0.6 °C since the late 19th century (Houghton *et al.*, 1996) and a 0.3 °C increase in Britain since the 1970s (Hulme & Barrow, 1997a). This is believed to be a result of anthropogenic emissions of certain gases, predominantly carbon dioxide, that have resulted in an enhanced "greenhouse effect" in the global atmosphere (Houghton *et al.*, 1996).

The observed decrease in daily and extreme annual temperature range in the long-term record is interesting, considering the absence of any trends in the mean. This implies that both maximum and minimum temperatures have been moderated. What is the potential importance of these changes for the vegetation of Widdybank Fell? Over the period between the two vegetation surveys (taken to be 25 years) there has been a decrease in daily temperature range of 0.41 °C and a decrease in extreme annual temperature range of 2.25 °C. The decrease in daily temperature range is predominantly a seasonal effect during winter and spring. These changes to some extent are similar to the changes in local climate produced by Cow Green Reservoir, particularly the implied moderation of minima. However the lack of difference between the records from Widdybank Fell and Moor House during the period of overlap (1968-1979) rule out the reservoir as a causal factor of these changes. In addition, the magnitude of the effect produced by the reservoir is considerably greater; grass minimum temperatures have been moderated by c. 1 °C all year round, and during extreme periods of cold at Moor House, the reservoir was moderating grass minimum temperatures at Widdybank by up to 10 °C.

### *6.3.3 Changes in seasonality of rainfall*

Under future global warming scenarios, in addition to an increase in mean temperatures, rainfall is predicted to become more seasonal. For example, using the HADCM2 SUL global climate model, precipitation in Northern England is predicted to increase by 0-2 % in winter and decrease by 2-4 % in summer between 2035 and 2064, compared to mean precipitation over the period 1961-1990 (Raper *et al.*, 1997).

Analysis of rainfall and streamflow data over the period 1953-1996, predominantly from Moor House (but using the Widdybank record for the period 1980 to May 1991) has indeed shown a trend towards increased seasonality, with drier summers and wetter winters (Burt, Adamson & Lane, 1998). This trend has also been seen using the rainfall record at Durham observatory since 1881 (Burt *et al.*, 1998) and at other regional stations (Jones & Conway, 1997). The summer of 1995 was the driest on record at Durham since 1881 and was the second driest at Moor House since 1953. 1996 was the third driest year at Moor House.

The increased seasonality in rainfall, and especially the dry summers of 1995 and 1996, could potentially explain some of the changes in bryophyte abundance between the two vegetation surveys. Leafy liverworts, in particular, are very drought sensitive. Although some of the survey was carried out in the wetter year of 1997, it is possible that bryophyte populations could still have been suffering from the effects of the previous two summers. In contrast, the years over which the baseline survey of Jones was carried out (1967-1969) were probably unexceptional in terms of total annual rainfall. Data for 1967 were not available at Widdybank, but 1968 and 1969 were ranked as the 10th and 15th driest years, respectively, out of the 28 year record. There is little purpose in subdividing these years further into seasons as it not known exactly when in each year Jones (1973) carried out her survey. In any case, she may have spent up to eight months in the field each year (Margaret Bradshaw *pers. comm.*). Although abundance of bryophytes might be affected by dry summers, it seems unlikely that such conditions would result in the actual loss of species. Even in the driest summer, it would be expected that there would be a number of moist microhabitats that would enable survival. From the available evidence, therefore, differences in rainfall may account for some of the reduction in bryophyte abundance between the two vegetation surveys, but is unlikely to be responsible for the observed species losses.

### 6.4 Atmospheric carbon dioxide

The elevated concentrations of carbon dioxide in the atmosphere over the last century have resulted largely from fossil fuel combustion (Houghton *et al.*, 1996). In addition to producing an enhanced "greenhouse effect" increased $CO_2$ concentrations can also affect plants directly. Experiments under controlled environment conditions have demonstrated that increased concentrations of $CO_2$ produces increased rates of photosynthesis and growth in many plant species with $C_3$ metabolism (Hunt *et al.*, 1991). However the magnitude and type of response to $CO_2$ enrichment varies interspecifically (e.g. Hebeisen *et al.*, 1997; Whitehead, Caporn & Press, 1997). Certain plant functional types may however share similar characteristics in their response to enrichment (Hunt *et al.*, 1991; 1993) with competitors *sensu* Grime (1977) the most responsive to elevated $CO_2$. Genetic variability within a species may also be important. Wulff and Alexander (1985) found wide variation in the response of four genotypes of *Plantago lanceolata* to $CO_2$ enrichment.

Short-term and long-term effects of enrichment may be different. Many plants eventually become acclimated to elevated $CO_2$ concentrations, with the result that photosynthesis is downregulated (e.g. Sage, Sharkey & Seeman, 1989). This acclimation has also been observed at the community level. Wolfenden and Diggle (1995) found rates of photosynthesis increased by 50 % in upland limestone grassland monoliths grown in elevated $CO_2$ concentrations in spring and summer, but at the end of the growing season rates of photosynthesis had returned to the equivalent of ambient rates. As a result, above ground productivity was unaffected. The effects of $CO_2$ enrichment on plants will also vary when temperature, light or availability of water or nutrients is sub-optimal. The response in terms of net primary productivity to elevated $CO_2$ by plant species when these factors are limiting differs interspecifically (Newton, 1991). Thus competition where resources are limited may mean that effects in the field are substantially different to those observed under controlled conditions.

The likely long-term effects of $CO_2$ enrichment on semi-natural ecosystems are largely unknown at present (Mooney *et al.*, 1991; Körner, 1995) due to the confounding effects described above and the obvious dangers of extrapolating from short-term studies. Some experiments on semi-natural ecosystems are in progress, for example the Bog Ecosystem Research Initiative (BERI) (part of the EU Framework IV Terrestrial Ecosystem Research Initiative) using Free Air Carbon dioxide Enrichment (FACE) technology. Realistically, such experiments need to run for many years to allow the potential for acclimation and thus to indicate what the ultimate outcome of $CO_2$ enrichment will be (Woodward, Thompson & McKee, 1991). In the uplands, where plants are often strongly nutrient and temperature limited, they may have fewer sinks (tissues importing a requirement for growth) for increased photosynthate and thus the potential effects of elevated $CO_2$ may be reduced (Mooney *et al.*, 1991).

Given the number of other changing environmental factors on Widdybank Fell it is difficult to attribute changes in species abundance directly to increased $CO_2$ concentrations. However this is certainly a factor that may gain increasing importance in future as atmospheric concentrations are predicted to increase. (Houghton *et al.*, 1996).

## *6.5 Atmospheric deposition of pollutants*

### *6.5.1 Summary of the different atmospheric pollutants and the relative importance of their effects*

This section considers whether the observed changes in the vegetation on Widdybank Fell may have been caused by deposition of atmospheric pollutants. In Britain as a whole, a number of different pollutants are currently deposited onto soil and vegetation. These include oxides of sulphur and nitrogen as well as ammonia. Deposition occurs in precipitation (wet deposition), through the dissolving of gases onto moist vegetation (dry deposition) and through droplet capture from fog or cloud (occult deposition). In upland areas, with relatively high precipitation levels (and higher incidence of "low" cloud) the pollutant load is generally higher than in the lowlands (Vincent *et al.*, 1996).

Atmospheric sulphur dioxide ($SO_2$) originates mainly from the combustion of fossil fuels and also from volcanic eruption. It may be deposited as sulphuric or sulphurous acid and is currently the major contributor to acid rain (Moore, Chaloner & Stott, 1996). Anthropogenic emissions of $SO_2$ in Europe rose from around 10 million tonnes per year at the turn of the century to a peak of around 40 million tonnes per year in the 1970s (Ågren, 1993). Concern about the effects of acid rain on the environment, particularly following acidification of European forests and lakes (e.g. Elsworth, 1984) resulted in efforts to control emissions, which fell to around 35 million tonnes per year in the early 1990s (Ågren, 1993).

Nitric oxide (NO) and nitrogen dioxide ($NO_2$) are of mainly anthropogenic origin, from the high temperature combustion of fossil fuels but also occur through natural processes such as nitrification and denitrification (Hornung, 1994). When of anthropogenic origin they are often emitted from a so called "point source" e.g. a factory chimney. Atmospheric ammonia ($NH_3$) is mostly derived from agriculture, particularly from high concentrations of animal slurry via decomposition of urea (Pearson & Stewart, 1993). This is an example of a "non-point source" i.e. of diffuse origin. Ammonia is of particular importance as a pollutant of upland areas because uplands are most often surrounded by agricultural (rather than urban) development and most ammonia is deposited close to its source of emission (Pearson & Stewart, 1993). NO and $NO_2$ contribute to the problems of so called "acid rain" and are often deposited as nitric acid (Moore *et al.*, 1996). Nitrification of the ammonium ion in soil produces hydrogen ions, so can also contribute to soil acidity (Bakker & Berendse, 1999). Wet deposition of total inorganic nitrogen averaged 6.9 kg N $ha^{-1}$ for the years 1964-1966 at Moor House (Gore, 1968) and had risen to 25 kg N $ha^{-1}$ by 1990 (RGAR, 1990).

Atmospheric deposition data have been collected at the meteorological station at Widdybank Fell since 1986, in the form of bulk deposition using a "bulk collector". Figure 6.1 shows concentrations of sulphate (non-marine origin), nitrate-N and ammonium-N ions deposited in bulk precipitation at this site. Interannual variation is high, but sulphate loads appear to be decreasing, whilst ammonium loads are increasing. The overall acid load ($H^+$ concentration) is apparently declining. In terms of actual deposition, for 1996 the total loads deposited were 13.7 kg $ha^{-1}$ of non-marine sulphur, 3.9 kg $ha^{-1}$ of nitrate-N and 4.2 kg $ha^{-1}$ of ammonium-N.

What effects do these pollutants have on vegetation and can they account for any of the observed changes in the vegetation at Widdybank? The role of atmospherically deposited nitrogen as a soil nutrient will be considered first, followed by the effects of acid deposition.

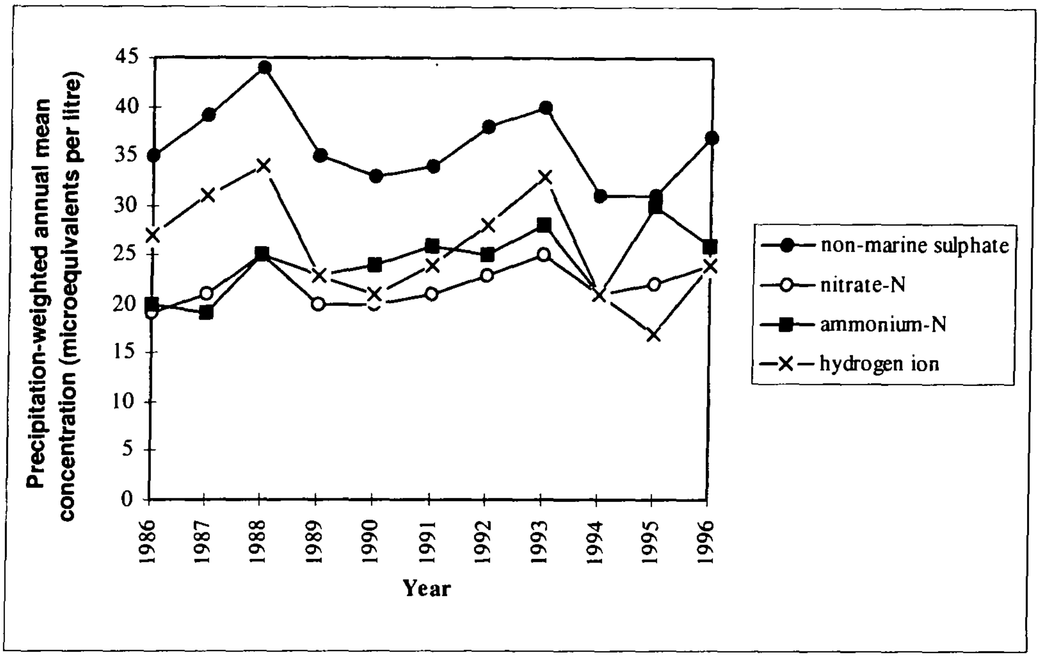



**Figure 6.1 Precipitation-weighted annual mean concentrations of deposited ions at Widdybank Fell, 1986-1996. Data from Vincent *et al.* (1996).**

In nutrient-poor upland soils, the nitrogen supply from atmospheric deposition is of potential significance for plant growth. Loads of nitrogen currently deposited in the UK are comparable to the mineralisation rates in many non-agricultural soils (Pastor, Stillwell & Tilman, 1987; Morecroft, Sellers & Lee, 1994). In the Netherlands, deposited loads of nitrogen are higher than in the UK, for example at least 50 kg N $ha^{-1}$ $yr^{-1}$ in South Limburg (Bobbink & Willems, 1987). Heathlands in the Netherlands have been declining, replaced by grassland, particularly by vigorous species like *Brachypodium pinnatum.* (Bobbink & Willems, 1987). Experimental addition of nitrogen to heathland has produced the same effect (Heil & Diemont, 1983) implying that nitrogen deposition is the most likely cause of this observed change.

Can deposition of nitrogen account for the observed changes in the vegetation at Widdybank? Although current loads of nitrogen deposition are certainly a source of concern, the vegetation on some of the sugar limestone soils has been demonstrated to be primarily phosphate rather than nitrogen-limited (Jeffrey & Pigott, 1973). Phosphorus deposition has not been routinely measured at Widdybank. However, records were taken in 1998 and weekly phosphate concentration in rainwater never exceeded trace levels, i.e. <0.05 mg litre$^{-1}$ (Ian Findlay, *pers. comm.*). Hence the atmosphere is unlikely to be an important source of P.

The term "critical load" is often used in pollution ecology. It describes the deposition load of a pollutant below which harmful effects on sensitive parts of an ecosystem are not known to occur, given the present state of our knowledge. (Hornung, 1994). Wilson, Wells and Sparks (1995) suggested a critical load for grazed, P-limited calcareous grasslands in the UK as between 42 and 55 kg N ha$^{-1}$ yr$^{-1}$. The critical load is hence not yet exceeded at Widdybank for this particular habitat type.

There was also no evidence from the vegetation survey to suggest adverse effects of nitrogen deposition, at least for vascular plants. The heather cover on the limestone heath had increased in density, if not in extent (see Chapter 3) rather than declining, as would be suggested as the long-term response under a high nitrogen input scenario. There was also no significant change in abundance in species associated with high soil nitrogen *sensu* Ellenberg (1988). However effects at the level of the individual plant may have occurred, even if they have not yet been of sufficient magnitude to affect competitive success. Concentration of nitrogen in *Calluna vulgaris* tissue has increased at Moor House by 35 % since the 1960s (Pitcairn, Fowler & Grace, 1991). It is possible that the disproportionate loss of stress-tolerant species could be a reflection of enhanced soil nitrogen status. However, this seems somewhat unlikely because some of the sugar limestone grasslands were shown to be strongly limited in inorganic phosphorus (Jeffrey & Pigott, 1973).

The noted decline in bryophyte diversity and lichen abundance could be an effect of nitrogen deposition however; particularly since similar changes have been observed elsewhere. For example, in areas of high atmospheric nitrogen deposition in the Netherlands there has been a noted impoverishment of the bryophyte and lichen flora (During & Willems, 1986). Of most relevance to the current study, however, are the changes seen at sites within the Moor House National Nature Reserve (Pitcairn *et al.*, 1991). One of the sites in particular shares some vegetation characteristics with the calcareous grasslands studied in the survey of Widdybank. It is an *Agrostis-Festuca* hummock/hollow complex on brown calcareous soils at Knock Fell (G. R. NY 719311, 747 m a.s.l.). Grazed and ungrazed plots have been monitored there since 1962. Both have shown a systematic decline in bryophyte and lichen diversity since that time. The species lost from the grazed plots do not appear to share a particular soil pH preference. This is the same change as seen for the bryophytes and lichens at Widdybank. Bryophytes and lichens are sensitive to acid deposition (e.g. Gilbert, 1970). However it might be expected in this case that if the acid component of the pollution was most important then calcicole species would be more likely to decline.

A study of bryophyte tissue nitrogen content was carried out by Pitcairn *et al.* (1991) using both recent and historic (herbarium) samples. Tissue nitrogen contents were similar in the 1950s for samples from four British sites. By 1989, however, there had been a significant increase in tissue nitrogen concentration at the sites receiving high inputs of atmospheric nitrogen. Most strikingly, tissue nitrogen content had increased by 63 % in *Sphagnum* species at Moor House. There is evidence from the Southern Pennines (an area subject to extreme atmospheric pollution) that ombrotrophic *Sphagnum* species are receiving supra-optimal amounts of atmospheric nitrogen (Lee, Tallis & Woodin, 1998). Although this is an extreme example, there is clearly the potential for atmospheric deposition to cause deleterious effects in other bryophyte or lichen species elsewhere in Britain.

Thus it seems likely that the observed loss of some bryophyte and lichen species is primarily a response to an increased atmospheric supply of nitrogen acting as a nutrient. The dry summer of 1996 may have had some impact on bryophyte populations recorded at Widdybank. However the similar changes seen through the long-term monitoring of plots at Moor House imply that the observed changes at Widdybank are probably more than merely a seasonal effect.

Although annual acid load in precipitation at Widdybank may have decreased, there is still the potential for a cumulative effect of acid deposition on soil and vegetation. The disproportionately high decline in the calcareous noda of species preferring high pH has already been described in Chapter 4. This change seems most likely to be a response to an increase in soil acidity. Equally, the increase in cover and density of *Calluna vulgaris* bushes seen in the limestone heath could suggest that soil acidification has occurred, which would favour this species. Hence it was clearly of value to carry out some *in situ* soil analysis. This is described in the next section.

### *6.5.2 Investigation of changes in soil pH at Widdybank Fell*

Increases in the acidity of mineral soils in the uplands have previously been reported (e.g. by Kuylenstierna and Chadwick (1991) for soils in north-west Wales between 1957 and 1990). However, the study of most relevance to the present investigation was that carried out by Adamson *et al.* (1996) (see Chapter 4). These workers found that mineral soils at Moor House and in the Upper Teesdale NNR had increased in acidity since the period 1963-1973, particularly in the organic and A horizons.

Notwithstanding these results, it was desirable to focus more closely on the grasslands of particular interest to this study. The thesis of Jones (1973) gives soil analysis data from a selection of the quadrats used in the vegetation survey. Ideally, a complete reanalysis of soil properties in each of the noda on Widdybank Fell should have been carried out, re-examining characteristics such as cation exchange capacity and levels of organic and inorganic nitrogen and phosphorus. This was unfortunately outside the scope of this thesis and the examination was confined to a study of soil pH (and loss on ignition) in selected noda only. Some of the quadrats used for soil sampling by Jones (1973) were those that had been repositioned for the present survey. It was possible to sample from 11 quadrats, in Noda 3, 4, 5, 7 and 21. The original analyses used six (15.2 cm long and 2.5 cm diameter) cores taken from each quadrat and bulked before analysis. Where quadrats contained hummock/hollow complexes, each topographic type was examined separately. The same procedures were used for this investigation. In addition, each soil core was analysed separately as well as in the bulked sample to provide a measure of variation between samples. As for the survey of Jones, soil pH analysis was carried out on air-dried samples and 10 g sample was mixed with 25 ml of distilled water. The samples were analysed after 30 minutes (time period not given by Jones, but followed the method of Hornung 1968) using a pH meter (Wissenschaftlich-technische 192, Germany). Loss in dry weight on ignition was also determined. Air dried samples (5 g) were dried at 105 °C and weighed, then reweighed after 16 hours at 375 °C, to determine percentage weight loss. This was the same method as described by Jones (1973) although her original sample weights were not given.

**Results**

The pH data from the survey of Jones and the present survey are given in Table 6.4. Figure 6.2 shows a comparison of soil pH between the two sampling dates, based on the data from the bulked samples. Overall soil pH has decreased; this is especially pronounced for the calcareous soils. This result is surprising as the soils which were most base-rich should have been best able to neutralise the incoming acidity. It is possible that this result is an artefact of measurement due to differences in methodology (i.e. the use of different pH meters). The differences in soil pH between the two sampling dates were compared using a paired t-test after converting the pH to $H^+$ concentration using the formula $1 \times 10^6$(1/antilog of the pH ) (Jeffrey, 1987). The differences in soil pH were not significant. As described above, a more detailed comparison of the present-day condition of the soils of Widdybank Fell, taking a greater number of samples across the fell would be desirable.

The data for percentage loss on ignition from the survey of Jones (1973) and the present survey are given in Table 6.5. Figure 6.3 shows a comparison of percentage loss on ignition between the two sampling dates based on the data from the bulked samples. Overall, the content of organic material in the soils has increased. Of the 15 sets of samples, ten had increased in their organic content

**Table 6.4 pH data from Jones (1973) compared with data collected in 1998 (this study).**

| Nodum | Quadrat | Soil type (Jones 1973) | pH from Jones (bulk sample only) | pH in 1998 | | |
|---|---|---|---|---|---|---|
| | | | | bulk sample | median (n=6) | range |
| **3** | 107 | rendzina β | 7.2 | 7.5 | 7.6 | 0.18 |
| **4** | 97 | shallow brown earth | 5.4 | 4.9 | 4.7 | 2.51 |
| | 102 | shallow brown earth | 5.4 | 5.4 | 5.6 | 2.27 |
| **5** | 115 | rendzina β | 7.7 | 7.4 | 7.4 | 0.83 |
| | 120 (hummock) | rendzina β | 8.0 | 6.8 | 6.8 | 1.43 |
| | 120 (hollow) | rendzina β | 7.9 | 7.5 | 7.6 | 0.19 |
| | 134 | rendzina β | 6.8 | 6.9 | 6.9 | 0.75 |
| | 138 | rendzina β | 7.5 | 6.6 | 6.6 | 0.98 |
| **7** | 65 (hummock) | brown calcareous/ brown earth | 7.7 | 7.5 | 7.5 | 0.29 |
| | 65 (hollow) | brown calcareous/ brown earth | 7.5 | 7.4 | 7.5 | 0.33 |
| | 81 (hummock) | (peaty) gley | 6.3 | 6.3 | 6.3 | 0.34 |
| | 81 (hollow) | (peaty) gley | 6.0 | 6.3 | 6.2 | 0.43 |
| | 112 | rendzina β | 7.8 | 7.2 | 7.3 | 0.83 |
| **21** | 121 (hummock) | rendzina β | 6.2 | 5.5 | 5.7 | 1.32 |
| | 121 (hollow) | rendzina β | 5.3 | 5.4 | 5.5 | 0.56 |

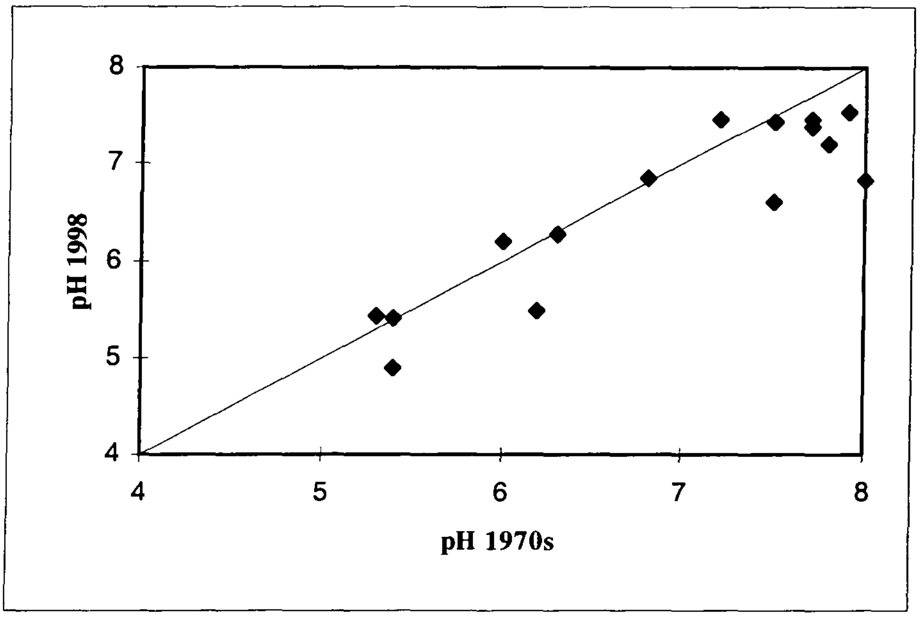



**Figure 6.2 A comparison of soil pH between the survey of Jones (1973) and the present survey in 1998. The 1:1 line is included for reference.**

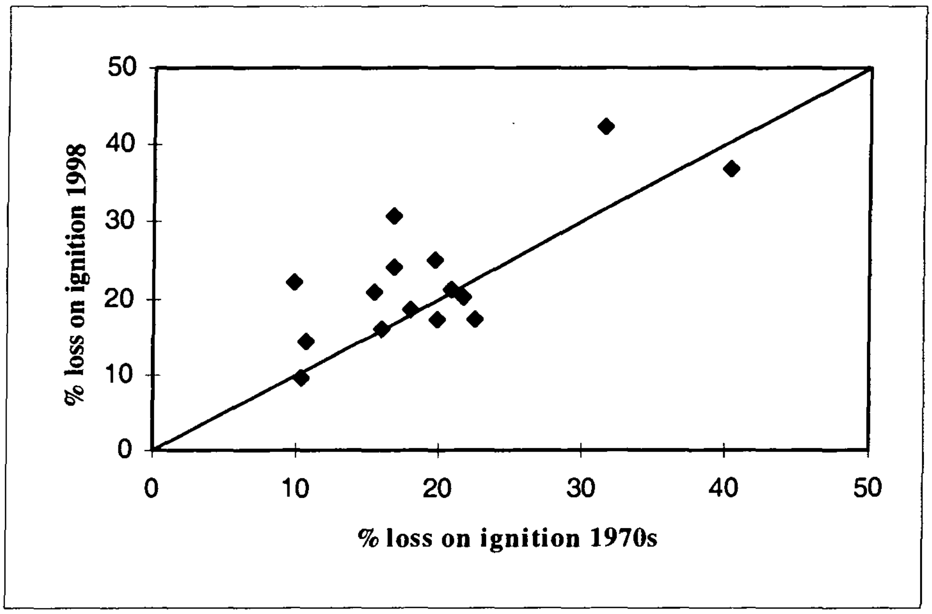



**Figure 6.3 A comparison of percentage loss on ignition between the survey of Jones (1973) and the present survey in 1998. The 1:1 line is included for reference.**

**Table 6.5 Percentage loss on ignition data from Jones (1973) compared with data collected in 1998 (this study).**

| Nodum | Quadrat | Percentage loss on ignition from Jones (bulk sample only) | Percentage loss on ignition in 1998 | | |
|---|---|---|---|---|---|
| | | | bulk sample | mean (n=6) | standard error |
| **3** | 107 | 22.56 | 17.28 | 14.68 | 1.74 |
| **4** | 97 | 16.78 | 23.99 | 23.76 | 2.22 |
| | 102 | 21.67 | 20.13 | 19.48 | 1.06 |
| **5** | 115 | 10.36 | 9.51 | 10.57 | 1.73 |
| | 120 (hummock) | 9.82 | 22.06 | 21.29 | 3.40 |
| | 120 (hollow) | 10.62 | 14.43 | 16.02 | 1.81 |
| | 134 | 19.83 | 17.28 | 19.60 | 1.55 |
| | 138 | 19.65 | 24.95 | 25.95 | 1.18 |
| **7** | 65 (hummock) | 17.89 | 18.75 | 20.58 | 0.96 |
| | 65 (hollow) | 20.90 | 21.04 | 21.83 | 1.44 |
| | 81 (hummock) | 40.31 | 36.83 | 35.40 | 2.09 |
| | 81 (hollow) | 31.60 | 42.20 | 40.64 | 0.68 |
| | 112 | 15.90 | 15.93 | 17.34 | 1.61 |
| **21** | 121 (hummock) | 15.40 | 20.96 | 20.19 | 0.77 |
| | 121 (hollow) | 16.71 | 30.83 | 19.49 | 0.95 |

between sampling dates. The mean change for all 15 samples was an increase of 16 %. There was no overall difference between hummocks and hollows in terms of change in soil organic content. Differences between the two sampling dates were compared using a paired t-test and were also not significant; in this case this is probably due to the relatively small sample size available.

**Discussion**

The general increase in soil acidity observed is consistent with the findings of Adamson *et al.* (1996) on sites at Moor House and Upper Teesdale. The cumulative effects of acid deposition are most likely to be responsible. The results above must be treated with caution, however, because of the apparent differences between sampling dates being greater for the calcareous soils.

Notwithstanding the caution with which the results obtained above must be treated, some change in soil properties resulting from acid deposition is the most obvious explanation for the reduction of calcareous soil preferring species on the limestone grasslands. Soil pH in the range 4.0-8.0 is not considered to have a direct effect on plant growth (Jeffrey, 1987). However there may be important secondary effects. Availability to plants of soil nutrients and toxic metals can be affected by soil pH. For example, calcium availability is reduced as soil pH falls below 7.0 (Truog, 1946, in Jeffrey, 1987). This may mean that calcicole species (i.e. those tolerant of high calcium) lose their competitive advantage when soil pH falls. In contrast, lead uptake by plants may be increased with decreasing pH. This is of potential importance because the sugar limestone soils are lead-rich (Jeffrey, 1971). Jeffrey hypothesised that the presence of lead was preventing phosphate uptake by species on the sugar limestone grasslands at Widdybank, so increased lead uptake may increase nutrient stress.

The increase in content of organic material in the soil is also consistent with the results of Adamson *et al.* (1996). Their study found an increase of 23 % in percentage loss on ignition throughout the soil profile. One reason for this increase in organic material in the soil suggested by Adamson *et al.* (1996) could be that the pH change has reduced the rate of decomposition. Alternatively, the increased concentrations of atmospheric carbon dioxide could have resulted in greater plant productivity and hence litter production. The ratio of carbon to nitrogen in plant tissues could also have increased, resulting in "poorer quality" litter that takes longer to decompose.

### 6.6 Conclusions

It is unlikely that there has been a significant change in grazing pressure on Widdybank Fell in the period between the two vegetation surveys. Although atmospheric concentrations of carbon dioxide have increased, it would be difficult to directly attribute the vegetation changes to this factor. The observed changes in regional daily and extreme annual temperature range share a similarity with the effects produced by Cow Green Reservoir in terms of the moderation of minima. However the effects of the reservoir on local climate are much greater.

The dry summers of 1995 and 1996 may account for some of observed losses in bryophyte abundance between the two vegetation surveys but is unlikely to be responsible for the loss in diversity. Increased atmospheric nitrogen deposition is probably the primary cause of the long-term decline in bryophytes. Acid deposition is the most likely cause of the loss of calcareous soil preferring species in the calcareous grasslands and could explain the increase in *Calluna* cover on the limestone heath.

### 6.7 Summary

- Four major environmental factors were examined as potentially responsible for the observed changes in the vegetation. These were changes in grazing pressure, regional climate, levels of atmospheric carbon dioxide and changes in atmospheric deposition of pollutants acting as plant nutrients and/or soil acidifiers.

- From the available evidence it was concluded to be unlikely that there had been significant changes in number of sheep grazing the fell over the period between the two vegetation surveys. Rabbit grazing is an important localised effect, but is unlikely to explain the observed changes in the vegetation across the entire fell.

- Some changes in regional climate have occurred in the recent past. There has been a reduction in daily screen temperature range of 0.71 °C and extreme annual screen temperature range of 3.97 °C over the period 1952-1995. These changes were observed using a combined record from Moor House and Widdybank. However previous workers had found no changes in mean screen temperatures so this implies an equal moderation of maxima and minima. In terms of the moderation of minima, these changes are similar to those produced by Cow Green Reservoir, but the effects of the reservoir on local climate are much greater. The observed increase in seasonality of rainfall (Burt *et al.*, 1998) is potentially of importance; the dry summers of 1995 and 1996 could account for some of the apparent loss in bryophyte abundance (but not diversity) between the two vegetation surveys.

- Atmospheric levels of carbon dioxide have increased this century. Although laboratory experiments have demonstrated a response in many plant species, the long-term effects on semi-natural habitats are unknown. It would hence be difficult to attribute any of the changes in vegetation on Widdybank Fell to this factor.

- Total deposited loads of atmospheric nitrogen are increasing at Widdybank. The vegetation changes that might be expected in a high nitrogen input system (as seen in the Netherlands) have not been observed at Widdybank, at least not for higher plants. This is probably because the vegetation on at least some of the sugar limestone soils at Widdybank is predominantly limited by inorganic phosphorus rather than nitrogen (Jeffrey & Pigott, 1973). However the observed loss in bryophyte diversity and lichen abundance is most likely to be an effect of nitrogen deposition.

- There has been an apparent overall reduction in annual acid deposition loads at Widdybank since the 1980s. However acidification of upland soils has been widely reported and soil samples taken from some of the quadrats on the fell, appeared to support this, although the results need to be treated with caution. The acidification observed in upland soils could reflect the cumulative effect of acid deposition, even if annual loads have declined. The effects of acid deposition provide the most likely explanation for the overall reduction in calcareous soil preferring species on the calcareous grasslands. It could also explain why the *Calluna vulgaris* on the limestone heath is apparently growing more successfully.

# 7. Microcosm experiment

## 7.1 Introduction

It has been shown that changes in the species composition of some of the vegetation types at Widdybank Fell have occurred since 1971. The demonstrated effect of Cow Green Reservoir on local temperature is one of the primary factors which could be responsible for these observed changes. This chapter examines the response to different temperature regimes by species and vegetation types shown to have changed in the period since reservoir construction.

One method of exposing the vegetation to different temperature regimes would have been *in situ* manipulation of ambient temperature using soil warming cables, but the lack of a mains electricity supply would have made this difficult. Other methods for temperature manipulation, such as erecting plastic tents over the vegetation, do not allow fine control of internal temperatures (e.g. Chapin & Shaver, 1985) and have the potential to alter other environmental variables such as humidity (Kennedy, 1995). Use of controlled environment rooms was a further option, but this is another step removed from the reality of field conditions.

The method ultimately selected was to move plants from Widdybank Fell to other areas that experienced different temperatures. The relative performance of such plants compared to plants remaining at Widdybank could then be assessed. As removal of intact turf monoliths was not acceptable in this National Nature Reserve, the method selected was to remove individual plants of a few representative species from the turf. These could then be reassembled as a simplified community in a microcosm. Microcosms have been defined as "small ecosystems in containers" (Beyers & Odum, 1993; Fraser & Keddy, 1997).

## 7.2 Methods

### 7.2.1 Site selection

Three sites were selected for the study in addition to Widdybank Fell (the only site with an impounded catchment). Great Dun Fell was at the highest elevation, with Moor House at a similar elevation to Widdybank, and Durham at the lowest elevation. These three sites thus provided a temperature gradient for the microcosm experiment. Moor House would be expected to be climatically very similar to Widdybank, but with some difference in temperature due to the lack of a nearby water body (and slightly higher elevation). All four sites had meteorological stations (Table 7.1). The microcosms were placed close to the recording instruments in order to obtain detailed information as to climatic differences between sites over the duration of the experiment.

An altitudinal gradient was considered the best method of producing different temperature regimes over a relatively short distance. Along the transect the length of the growing season (taken to be the period when mean temperatures exceed 5.5°C (Manley, 1968)) shortens considerably with altitude (Figure 7.1) as does the number of growing degree days (Table 7.1). These differences between sites would be expected to produce a discernible difference in plant growth. As the four sites are at a similar latitude, day length is virtually identical. However the east-west transect exacerbates the existing differences in annual levels of precipitation, resulting from the sites being at different altitude. Additionally there are altitudinal differences in wind speed. Both these factors needed to be taken into account during interpretation of results.

**Table 7.1 Site information for the four meteorological stations selected for the microcosm experiment. Climatic analyses are based on the years 1991-1995. Note: the Great Dun Fell daily mean temperature and daily rainfall data had many missing entries. The corresponding entries were hence removed from the records at the other stations. As a result, growing degree days and total rainfall will be an underestimate for all stations.**

| **Site** | **Durham** | **Widdybank Fell** | **Moor House** | **Great Dun Fell** |
|---|---|---|---|---|
| Grid reference of met station | NZ 267 416 | NY 818 298 | NY 758 328 | NY 710 322 |
| Latitude | 54° 46'N | 54°39.75'N | 54° 41.3'N | 54° 41.1'N |
| Longitude | 1° 35'W | 2° 7'W | 2° 23'W | 2° 27'W |
| Day length (hours) at summer and winter solstice | 17.05<br>6.95 | 17.03<br>6.97 | 17.03<br>6.97 | 17.03<br>6.97 |
| Distance above sea level (m) | 102 | 513 | 560 | 847 |
| Distance and direction from Widdybank met station (km) | 46.5<br>East-North-East | 0 | 5.7<br>North-West | 10<br>West-North West |
| Mean annual precipitation (mm) | 411 | 996 | 1210 | 2543 |
| Mean annual wind speed (knots) | 5.2 | 14.9 | 8.7 | 23.1 |
| Mean number of growing degree days (total number of degrees above 5.5°C accumulated across the whole year) | 1205 | 666 | 556 | 432 |

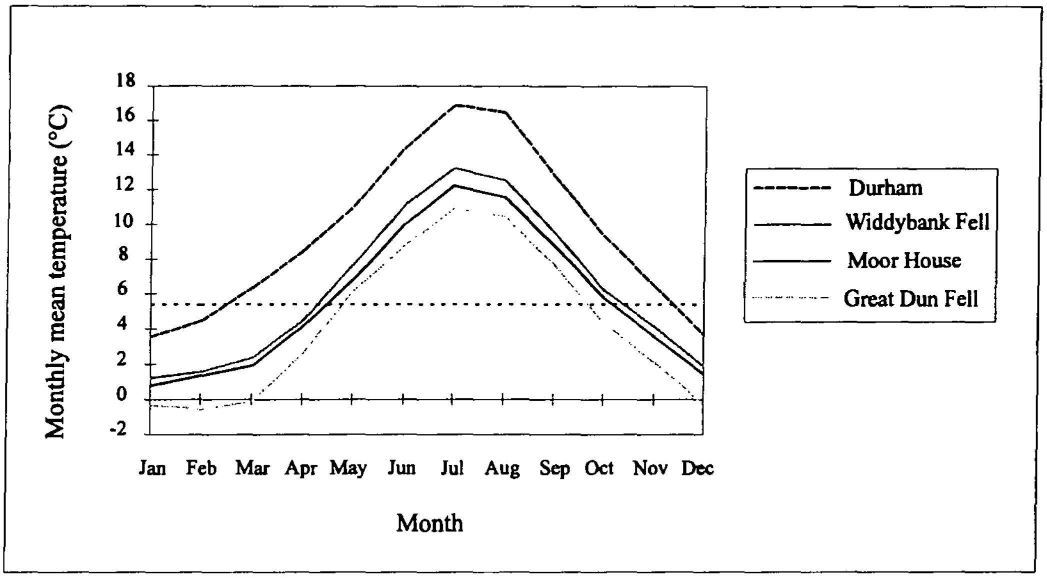



**Figure 7.1 Monthly mean temperatures at the four meteorological stations using data from 1991-1995. The fitted line at 5.5 °C indicates the theoretical threshold for the growing season (Manley, 1968).**

### *7.2.2 Selection of vegetation noda and individual species within them*

Two grassland types were grown in the microcosms, based upon:

1. Selected species collected from Nodum 33 (Order Calluno-Ulicetalia, acid grasslands: Nodum with *Danthonia decumbens*).
2. An amalgamation of selected species collected from Nodum 21 (Class Molinio-Arrhenatheretea, calcareous grasslands: Nodum with *Carex caryophyllea*) and Nodum 4 (Class Festuco-Brometea, calcareous grasslands: Nodum with *Calluna vulgaris*)

Microcosm nomenclature was based on the source of the plants used: i.e. Nodum 33 microcosms or Nodum 21 & 4 microcosms. The three noda used to provide species for the microcosms had been examined by Willis (1995) and changes in species composition found compared with the earlier survey of Jones (1973). Selection of the species within each nodum for use in the microcosms was also based on the survey of Willis (1995). Some of these were among the dominant species in the noda in terms of recording relatively high scores on the Domin scale (see Table 7.2; additionally Table (i) in Appendix D). Additionally, some were newly recorded or had changed in frequency or abundance compared to the survey of Jones; i.e. were species potentially more sensitive to climate change.

**Table 7.2 The species used in the two microcosm types. Mean Domin score for each species (from Willis, 1995) is shown, from which relative abundance in the microcosm was calculated. Changes in species frequency or abundance between the survey of Willis (1995) and the survey of Jones (1973) are also indicated, calculated using Mann-Whitney tests (more details in Appendix D, Table (i)). Changes in species frequency or abundance between surveys are indicated as species unchanged (u) now increased (+) decreased (-) new (N) or changing differently in frequency and abundance, respectively (+/- ) (* P≤0.05, ** P≤0.01). Refer to Chapter 3 for a more detailed explanation of these symbols.**

† relates to nodum of origin

| | **Nodum 33 microcosm** | | | **Nodum 21 & 4 microcosm** | | | |
|---|---|---|---|---|---|---|---|
| Species | Mean Domin score in Nodum 33 (Willis, 1995) | Change in frequency or abundance since the survey of Jones? | Number of plants used in each microcosm | Species origin (Nodum 4 or Nodum 21) | Mean Domin score in that nodum (Willis, 1995) | Change in frequency or abundance since the survey of Jones? † | Number of plants used in each microcosm |
| *Achillea millefolium* | 1.8 | N** | 9 | 21 | 1.3 | u | 6 |
| *Agrostis vinealis* | | | | 4 | 0.6 | N | 3 |
| *Festuca ovina* | 8.1 | +* | 42 | 21 | 7.2 | +* | 34 |
| *Galium saxatile* | 2.8 | -* | 15 | | | | |
| *Thymus praecox* | 2.1 | N ** | 11 | 21 | 3.2 | -** | 15 |
| *Sesleria albicans* | | | | 4 | 4.9 | - | 23 |
| *Trifolium repens* | 2.5 | + | 13 | 21 | 2.1 | -* | 10 |
| *Viola lutea* | 2 | +/- * | 10 | 21 | 1.9 | - | 9 |

Relative abundance of each species in the field was calculated using the mean score on the Domin scale, including scores of zero. The inclusion of zero meant that the median could not be successfully used, although the mean was not an ideal measure either, as the Domin scale is non-parametric. However this was considered sufficient to provide a basic estimate of relative abundance.

One of the dominant species in Nodum 4, *Calluna vulgaris*, was excluded from the microcosms on grounds of difficulty of propagation and because it was the limestone grassland species in Nodum 4 that were of interest (NB components of this nodum were amalgamated with the limestone grassland Nodum 21).

Standard ecological information on the selected species can be found in Appendix C, Table (ii). It should be noted that the four sites along the altitudinal gradient are within the recorded ecological tolerance of these species. The species used are found in some lowland areas of Britain, although they may be more common in upland areas, often due to lack of successful competition against faster-growing species in more fertile lowland soils (or absence of a suitable soil type). All the species selected for the microcosms have also been recorded in Britain at altitudes above that of Great Dun Fell (847 m). A possible exception is *Viola lutea*, for which the climate at Durham may be marginal for survival. Although this species is found at sea level in Co. Clare, Ireland it is not recorded below 200 m in Derbyshire, near the southern end of its British range (Balme, 1954) probably due to its requirement for high humidity and relatively low summer temperatures.

### *7.2.3 Null hypotheses*

The major null hypothesis tested was that the performance of the species in the microcosms was not affected by their environment. Hence there should be no difference in growth between the four experimental sites. In addition, for the five species common to both microcosm types, there should be no effect of soil type i.e. the species should grow equally well in both the Nodum 33 and Nodum 21 & 4 microcosms (notwithstanding any effects from the different additional species present). These two null hypotheses were tested by repeated surveys on the microcosms using a point quadrat, over two growing seasons (Section 7.2.5 below).

### *7.2.4 Microcosm design, construction and situation*

Plants were collected from the three noda on Widdybank Fell between August and September 1996. Collecting from each nodum was carried out in a single area of between 25 and 50 square metres in size (see Appendix D for details of collecting sites). By collecting over a relatively small area in each nodum, plants of similar genetic character (some of which may have been clones) were selected. Such genetic uniformity is desirable in that the plants should respond similarly to environmental change (Evans, 1972). Also the study species will have experienced similar micro-environmental conditions prior to collection.

The collected plants were separated into small rooted pieces or tillers and planted in seed trays of washed sand at Durham Botanic Gardens. The trays were initially watered with a soil solution collected from the appropriate nodum, in order to inoculate the sand with indigenous soil micro-organisms. The plants were left to root until mid-November 1996. Some of the species used responded better to this method of propagation than others. Species that rooted particularly well were *Sesleria albicans*, *Festuca ovina*, and *Agrostis vinealis*. *Thymus praecox* subsp. *arcticus*, *Trifolium repens* and *Achillea millefolium* rooted satisfactorily but *Viola lutea* and *Galium saxatile* were less successful; in both these cases more plants had to be collected to make up sufficient rooted plantlets for the microcosms. There was also some difference in rooting success depending on where the plants originated. *Viola* appeared to produce better roots in plants collected from Nodum 33, whereas the *Achillea* from Nodum 33 rooted less well than those plants collected from Nodum 21.

Black plastic buckets obtained from a florist were used as the microcosm containers. The pots had a height of 25 cm and a rim diameter of 25 cm and tapered to a base diameter of 18 cm. Eight drainage holes of c. 1 cm diameter were drilled in each base. The outside of each pot was painted white using "Dulux weathershield" exterior undercoat in order to reflect solar radiation (in fact only the rim was ultimately exposed to the sun). The growth medium in the microcosms comprised soil collected from the fell, from Nodum 33 or 21 for the Nodum 33 and Nodum 21 & 4 microcosms respectively. Within these two noda, the same sites were used as for plant collection, and soil was obtained from molehills in order to minimise disturbance to the intact turf. The soil was well mixed before use in the microcosms. Use of homogenised soil resulted in the loss of any discreet soil profiles, the potential consequences of which are discussed later.

The average root depth of the turf in all three noda was around 10 cm (ascertained from sample soil cores). A selection of grits (See Table (ii) in Appendix D) of various sizes were placed in the buckets to ensure good drainage and to obtain an equivalent soil depth to that in the field. The depths of the different growing media in the buckets are shown in Figure 7.2. The pH of the soil was sampled shortly after microcosm assembly. In the Nodum 33 microcosms the median pH was 6.78 (with a range of 0.06; n=4) and in the Nodum 21 & 4 microcosms it was 6.95 (with a range of 0.11; n=4).

The size of the microcosm allowed 100 individual plants to be planted at a similar density to their occurrence *in situ*, plus a "guard row" of *Festuca* just inside the rim to avoid edge effects. As previously described, relative abundance of each species in the microcosm was based on their relative abundance in the field using the mean score on the Domin scale from Willis (Table 7.2, above). An alternative method would have been to use equal proportions of the species in each pot. This has the advantage that relative abundance of species may change quickly or noticeably to "equilibrium", but it would not have been practically possible to obtain enough of the less abundant species.

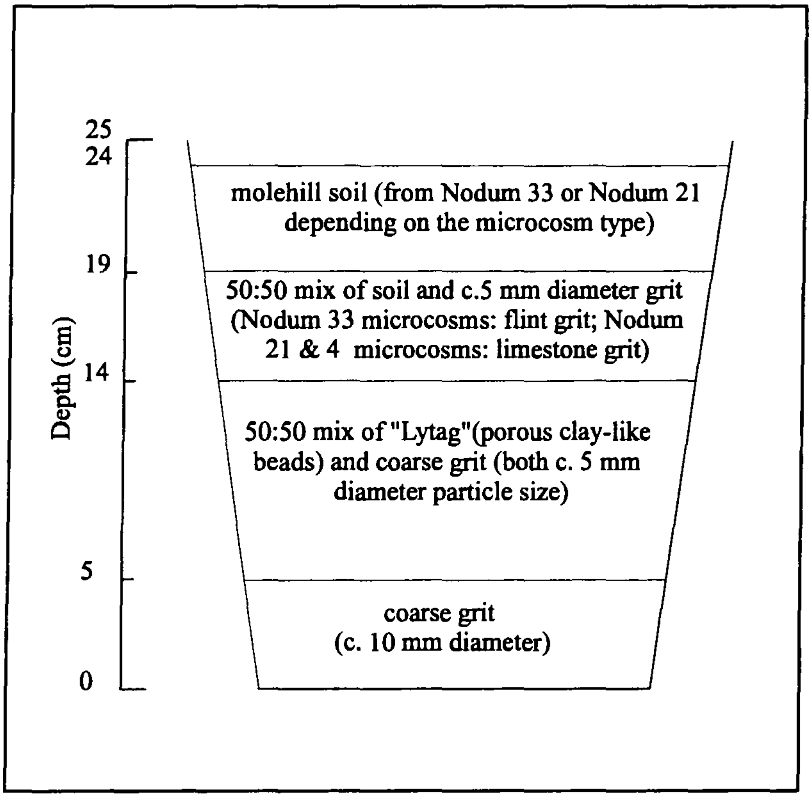



**Figure 7.2 Composition of the growing medium in the two microcosm types.**

The planting design was based upon a grid for the 100 plants where each plant was surrounded by six others. The different species were allocated positions so that no two plants of the same species touched (with *Festuca* as the exception, where necessary). For planting designs see Appendix D, Figure (i). Sixteen replicates of each of the two microcosm types were planted. Four microcosms of each type were then randomly assigned to the meteorological exclosures at Widdybank Fell, Moor House and Great Dun Fell. At Durham the microcosms could not be placed directly next to the recording instruments, but in an exclosure at a distance of 71 m west-south-west of them.

Microcosms were placed at the sites between 30th January and 18th February 1997. In order to help prevent strong fluctuations in soil temperature and to avoid the soil drying out (no additional watering was carried out) a wooden frame constructed from interlocking floorboards was erected round the pots and this filled with sand. Four positions in the frame had been randomly assigned to Nodum 33 microcosms and four to Nodum 21 & 4. This layout was consistent between sites, with individual microcosms randomly assigned to one of the four potential holes for its type. Pot orientation was also random. More details of pot arrangement in the frame are given in Appendix D. Details of replicate assignment to each site are given in Appendix D, Figure (ii).

As a result of concern about damage to the microcosms by grouse, netting was erected over the frames at each site from April to October 1997. In the second season there was evidence of rabbit damage in the exclosure at Moor House, so a permanent one metre high chicken wire fence was erected around the frames at each site.

### *7.2.5 Monitoring*

A point quadrat was used as the primary method for monitoring plant growth. These are widely used as an accurate way of estimating relative above ground biomass in microcosms (Naeem et al., 1994; Weiher & Keddy, 1995). The point quadrat consisted of two 26.5 cm diameter, 0.5 cm thick perspex discs bolted one above the other (20 cm apart) using four long steel screws in each "corner" that would fit inside the microcosm pot and act as feet. The discs had 100 numbered holes (c. 1 mm diameter) at intervals of 2 cm covering the area of the bucket with the experimental plants, but not the guard row. A sprung steel pin (c. 1 mm diameter) was used for recording vegetation touches (see Figure 7.3).

It was desirable, when making repeated measurements with the point quadrat over the experimental period, that pin touches on the vegetation would be in almost exactly the same position on each occasion. In order to achieve this, eppendorf tubes were placed in the pots, which acted as supports for the quadrat feet. In practice, however, some movement of these quadrat foot supports occurred and also movement of individual plants, for example as a result of frost-heave.

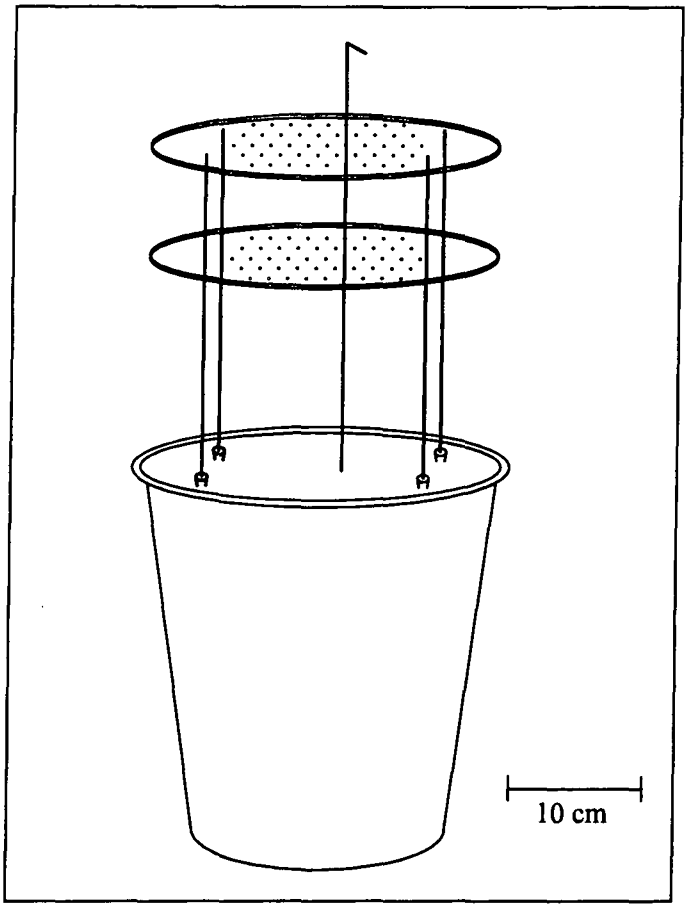



**Figure 7.3 Sketch diagram of the point quadrat, shown in position over a microcosm. Note the eppendorf tubes used as "feet" buried in the pot.**

Every "hit" by each pin on both live and dead plant parts was recorded. As well as recording which of the species had been hit by a particular pin, multiple hits by the same pin on different plants of the same species or on the same plant were also noted. There could clearly be a tendency for small-leaved plants to be relatively over-recorded using this method, but this was not a problem here as direct comparisons between growth of different species were not made (of little value because of the initial differences in planting density for each species). Any seedlings that emerged in the pot and were not of the study species were removed.

An initial point quadrat survey of the microcosms was carried out in January 1997 immediately after planting, in order to confirm that there was no initial difference in abundance of each species between the 16 replicate pots (see comments in results section, below). Subsequent recording of the pots in their experimental positions occurred at two-monthly intervals starting in April 1997 and continuing until August 1998. The four sites were normally visited within the first week of the month. The order in which they were visited on each occasion varied, being primarily dependent on vehicle availability and local weather conditions. Additionally, the pots were photographed during the first week of October in 1997 and 1998. A destructive harvest of the pots at the end of the study was not carried out, as it would provide little additional information to that obtained from the point quadrats; and also enables monitoring to be continued beyond the duration of this project.

### *7.2.6 Data analysis*

Climate data for the experimental period in 1997 and 1998 were compared between the four stations. Monthly mean temperatures and total rainfall over the experimental period were calculated. Unfortunately, due to large gaps in the Great Dun Fell dataset, some months had to be excluded completely, so monthly rainfall totals could not be calculated.

For each microcosm on each sampling date, the total number of live and dead "hits" by the 100 pins on each species was calculated. These figures were used as the basis for all subsequent analyses. Three levels of investigation were used to test the null hypothesis of no difference between species performance (i.e. number of live or dead hits) between sites:

1. Species performance between the four sites on individual sampling dates was compared using single-factor ANOVA. Additionally, t-tests were used to compare the number of hits between just two sites, Widdybank and Moor House, for each date.

2. Overall performance for each species over the experimental period was evaluated between the four sites by using single-factor ANOVA on the total hits for all sampling dates combined. Additionally, t-tests were carried out to compare species performance between Widdybank and Moor House.

3. Overall community performance over the experimental period was evaluated by combining hits on all species in each microcosm then testing for differences in performance between sites using ANOVA and t-tests as before.

The null hypothesis of no difference in species performance between the Nodum 33 and Nodum 21 & 4 microcosms (for the five species common to both microcosm types) was also tested, thus:

The total number of live and dead hits recorded for each of these species (combined for all sampling dates) was compared between Nodum 33 and Nodum 21 & 4 microcosms for each site using t-tests. As there were differences in initial number of each species planted in the two microcosm types (see Table 7.2, above) the totals were first standardised. For example, if 30 % more plants of a particular species were initially present in the Nodum 33 microcosm, the Nodum 21 & 4 microcosm had its respective total for that species increased by 30 % to correct for this.

### 7.3 *Results*

Figure 7.4 shows the monthly mean screen temperature at the four sites, for the period January 1997 to June 1998 (no data available at Great Dun Fell for July or August 1998 so these months were excluded at all sites). These data show a similar pattern to that observed in the five-year mean (Figure 7.1 above). The monthly mean temperature never fell below 5.5 °C at Durham so there was the potential for growth all the year round. In contrast, at Great Dun Fell, mean temperatures were only above 5.5 °C from the end of April to mid-September, with Widdybank Fell and Moor House having a longer season by two to three weeks. Table 7.3 below shows the difference in precipitation and growing degree days between sites over the experimental period. Great Dun Fell received around double the rainfall of Durham and had less than a third of the growing degree days.

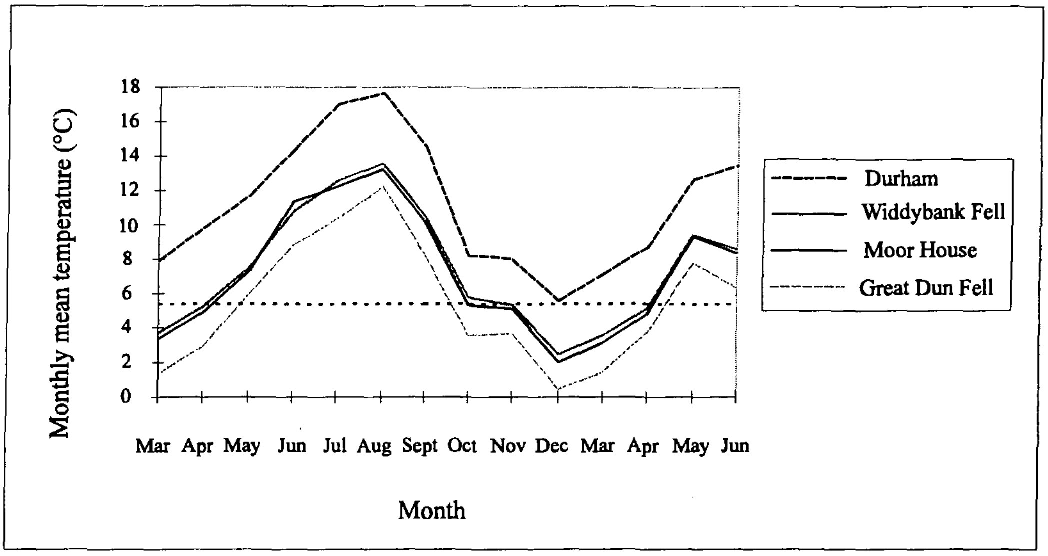



**Figure 7.4 Monthly mean temperatures at the four meteorological stations over the experimental period (January 1991 to June 1998). The fitted line at 5.5 °C indicates the theoretical threshold for the growing season (Manley, 1968). Note: months for which there were less than 10 daily entries were deleted at all sites.**

**Table 7.3 Climate data from the four stations over the experimental period (January 1997-June 1998). NB the Great Dun Fell data were incomplete for this period so as in Table 7.1 total precipitation and growing degree days will be underestimated at all sites.**

| **Site** | **Durham** | **Widdybank Fell** | **Moor House** | **Great Dun Fell** |
|---|---|---|---|---|
| Total precipitation (mm) | 749 | 1268 | 1275 | 1507 |
| Total growing degree days (calculated as in Table 7.1 above) | 1127 | 522 | 509 | 331 |

Plate 7.1 shows a Nodum 33 and a Nodum 21 & 4 microcosm just after planting in January 1997. Plate 7.2 shows the microcosms *in situ* at Great Dun Fell in their sand filled frame. Plates 7.3 shows representative Nodum 33 and Nodum 21 & 4 microcosms in October 1997 and October 1998 for Durham and Plate 7.4 shows the same for Great Dun Fell. The differences in growth between these two sites at the extremes of the altitudinal gradient are clear after one season. Compare especially the noticeable growth between 1997 and 1998 at Durham with the minimal growth at Great Dun Fell over this period.

### 7.3.1 *Relative performance between sites for each species on individual sampling dates throughout the experimental period*

Figures 7.5-7.17 show for each species in the two microcosm types, the mean number of live and dead hits over the duration of the experiment for each site. Results from single-factor ANOVAs on both live and dead hits examining differences between the four sites for each date are presented, as are results from t-tests comparing both live and dead hits between Widdybank and Moor House only. Multiple probability (Wigley *et al.*, 1987) was also calculated to take into account the number of tests performed. 117 of each type of test (e.g. ANOVA on live hits) were carried out in total: 13 combinations of species and microcosm type x 9 sampling dates (excluding the baseline survey in January 1997). For the 117 tests performed, the equivalent of $P \leq 0.05$ for an individual test is modified to $P \leq 0.00044$ (approximately).

It should be noticed firstly that there was no initial difference between the species composition of any of the pots between, or within, sites in January 1997 (the baseline survey). The exception to this, *Viola lutea* in the Nodum 33 microcosm, could be expected by chance alone considering the number of ANOVAs and t-tests performed (13 of each test i.e. one for each species for this date). This was not significant at the multiple probability level allowing for the 13 tests.

**Plate 7.1 One replicate of each of the two microcosm types: Nodum 21 & 4 (left) and Nodum 33 (right) shortly after planting in January 1997.**

**Plate 7.2 The microcosms *in situ* (here on Great Dun Fell). Note the point quadrat in position over a microcosm.**

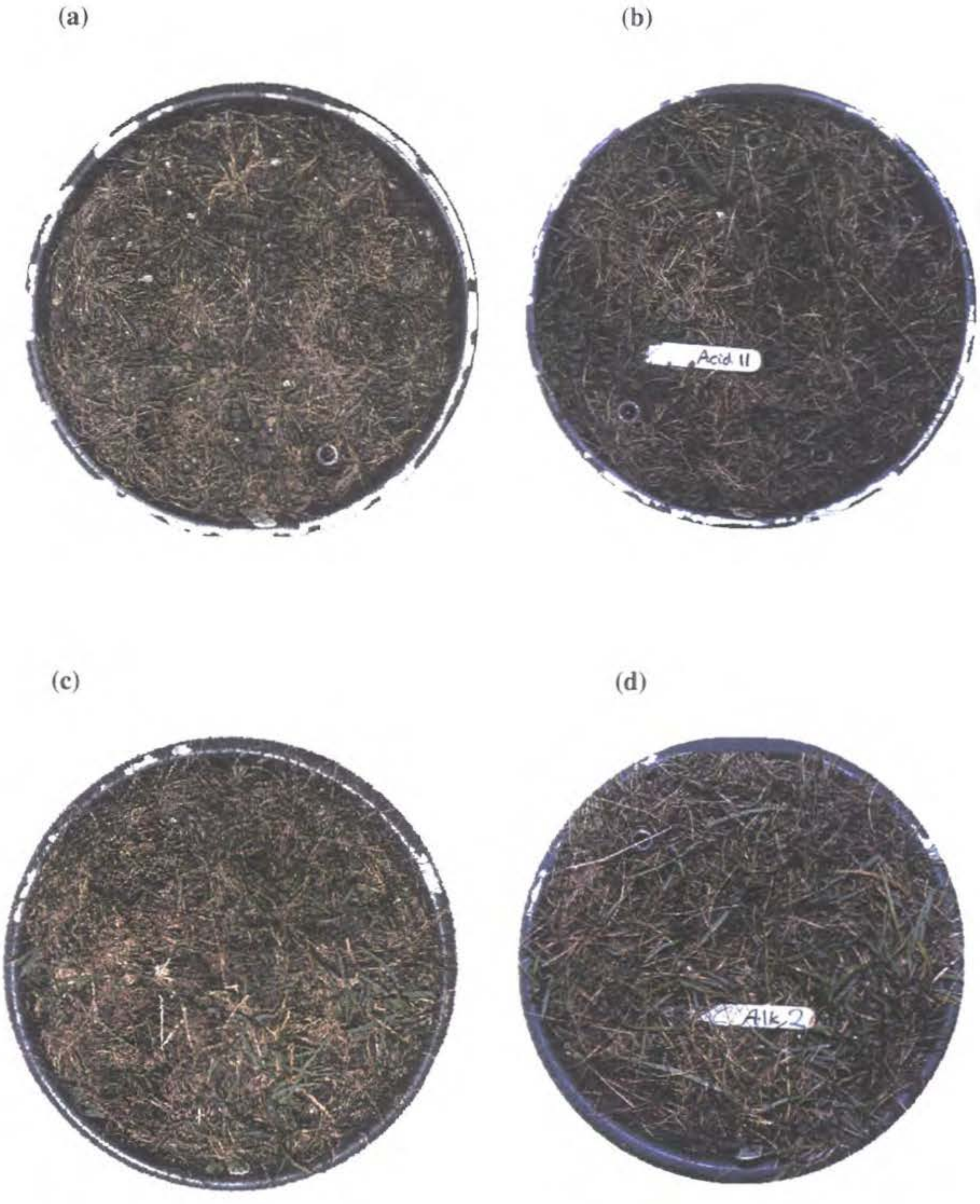



**Plate 7.3 Durham microcosms.**
**(a) Nodum 33 microcosm (replicate 11) in 1997; (b) the same microcosm in 1998.**
**(c) Nodum 21 & 4 microcosm (replicate 2) in 1997; (d) the same microcosm in 1998.**

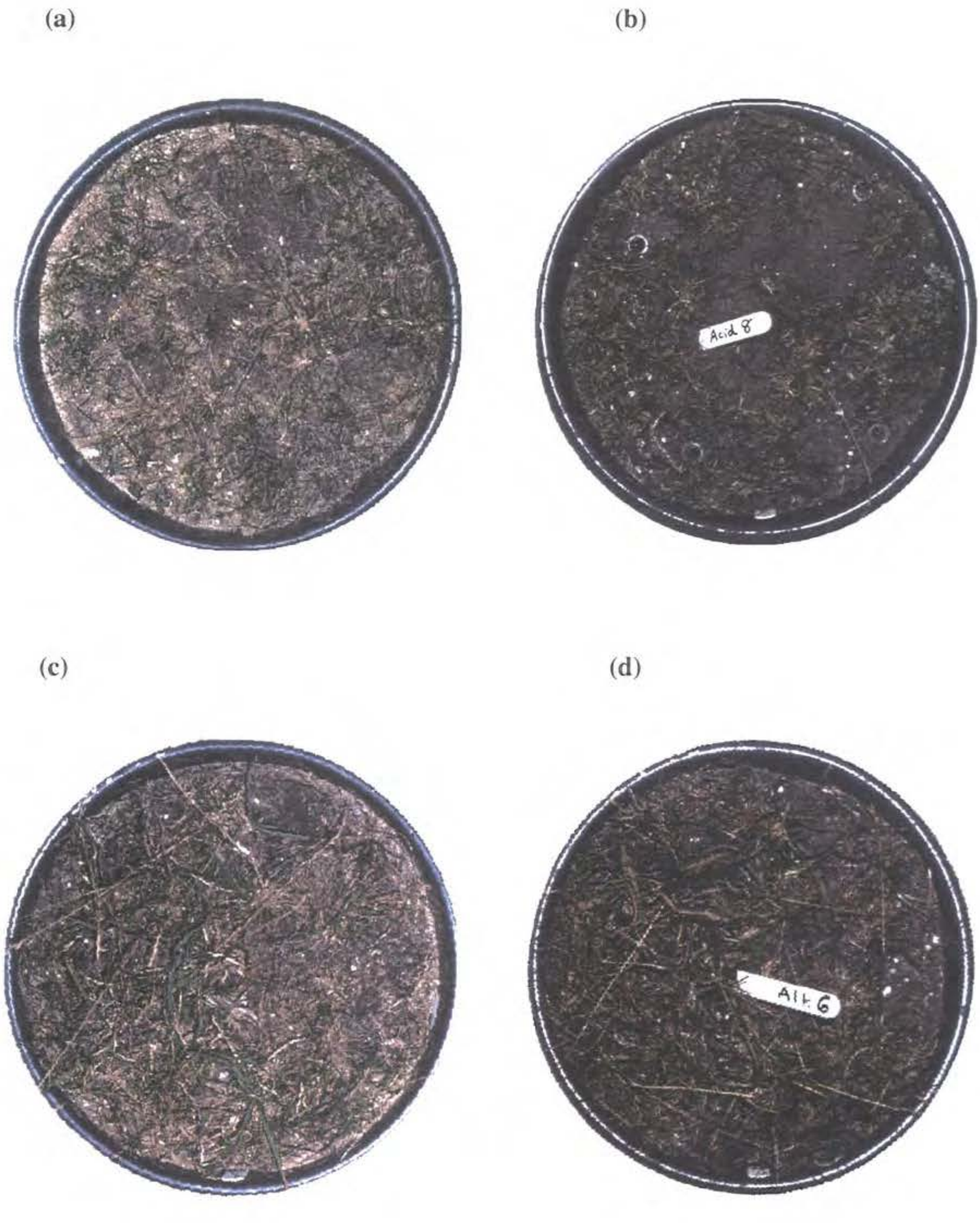



**Plate 7.4 Great Dun Fell microcosms.**
**(a) Nodum 33 microcosm (replicate 8) in 1997; (b) the same microcosm in 1998.**
**(c) Nodum 21 & 4 microcosm (replicate 6) in 1997; (d) the same microcosm in 1998.**

**Figures 7.5-7.17 Mean number of live (filled bars) and dead (empty bars) point quadrat hits per 100 pins on each species in the two microcosm types from January 1997 to August 1998. Significant differences between number of hits for the four sites (examined using ANOVA) and between Widdybank Fell and Moor House only (examined using t-tests) are shown (* P ≤0.05, ** P≤ 0.01, ***P≤ 0.05 at the multiple probability level). Note differences in scaling of the y-axis between species.**

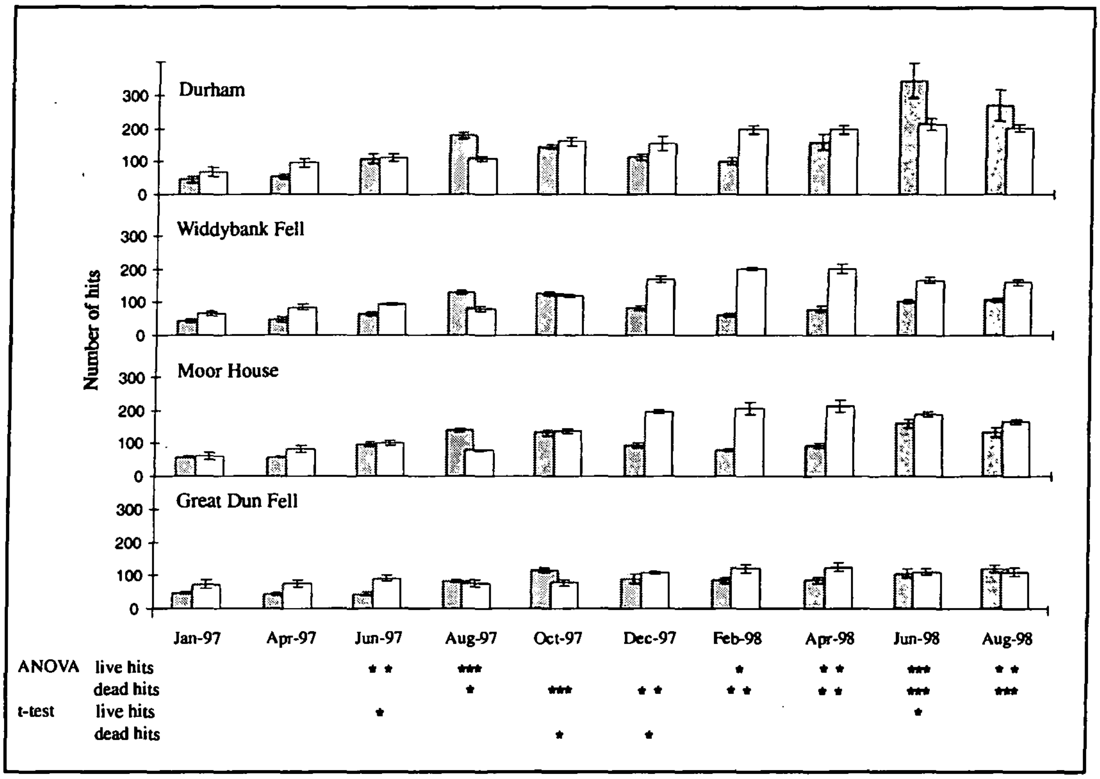



**Figure 7.5** ***Festuca ovina*** **- Nodum 33 microcosms.**

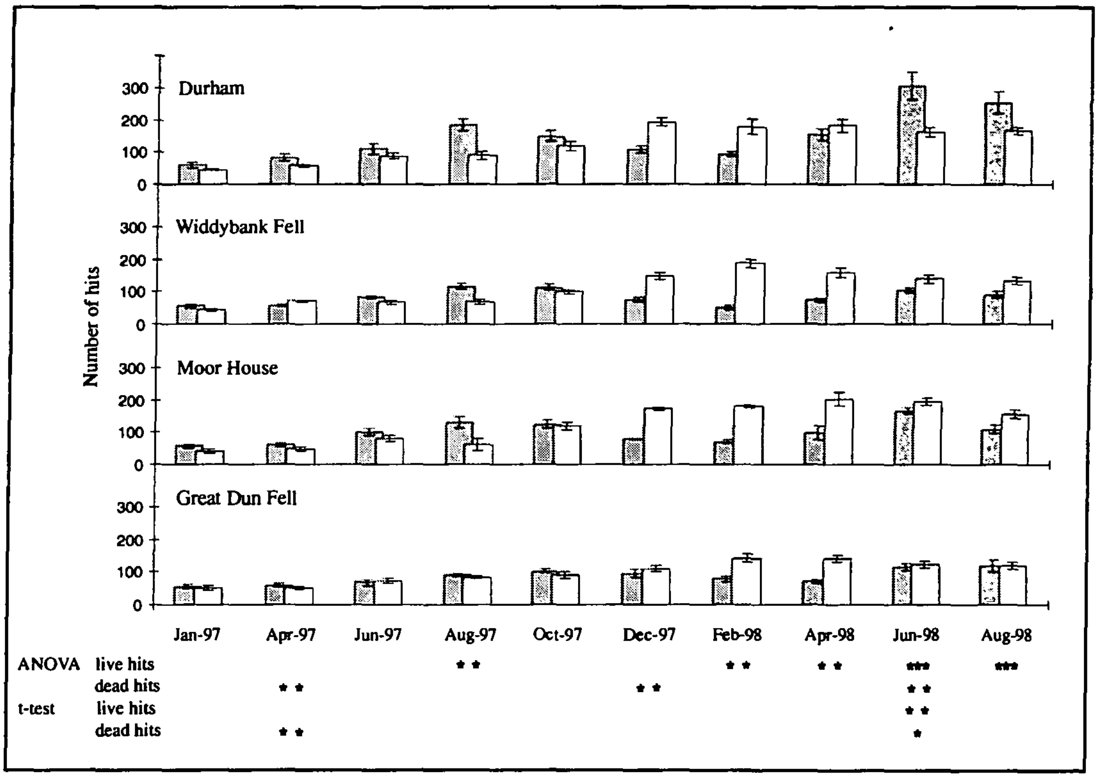



**Figure 7.6** ***Festuca ovina*** **- Nodum 21 & 4 microcosms.**

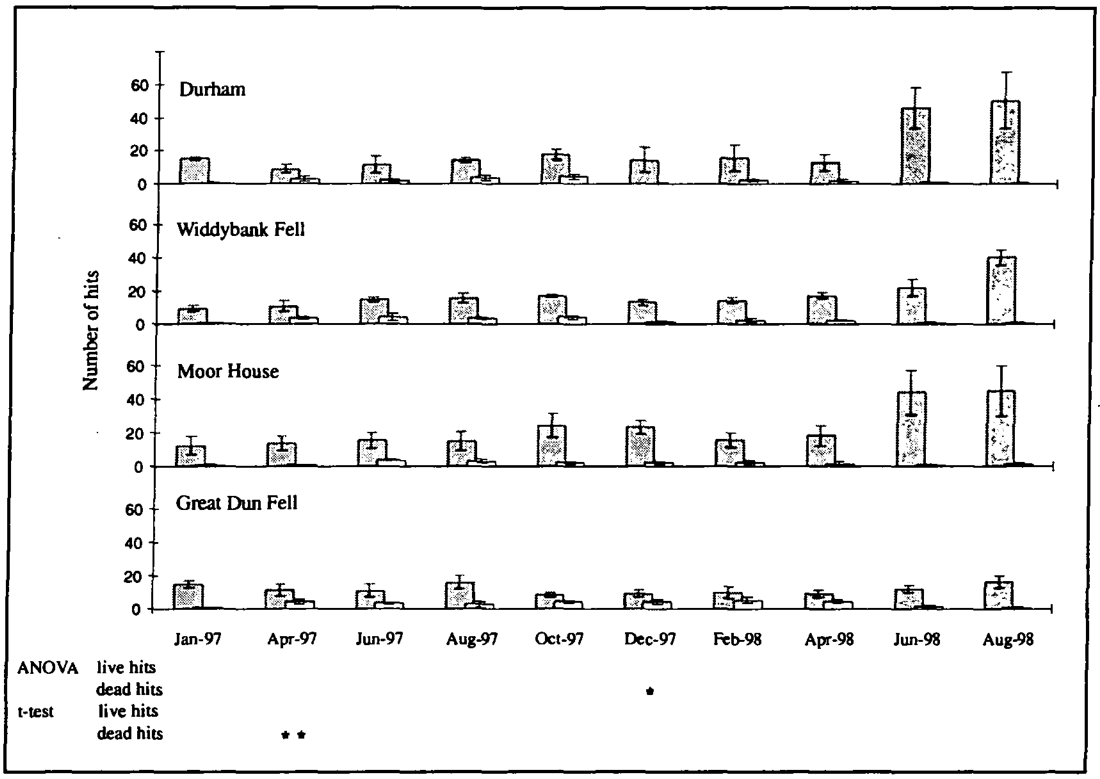



**Figure 7.7** ***Thymus praecox*** **subsp.** ***arcticus*** **- Nodum 33 microcosms.**

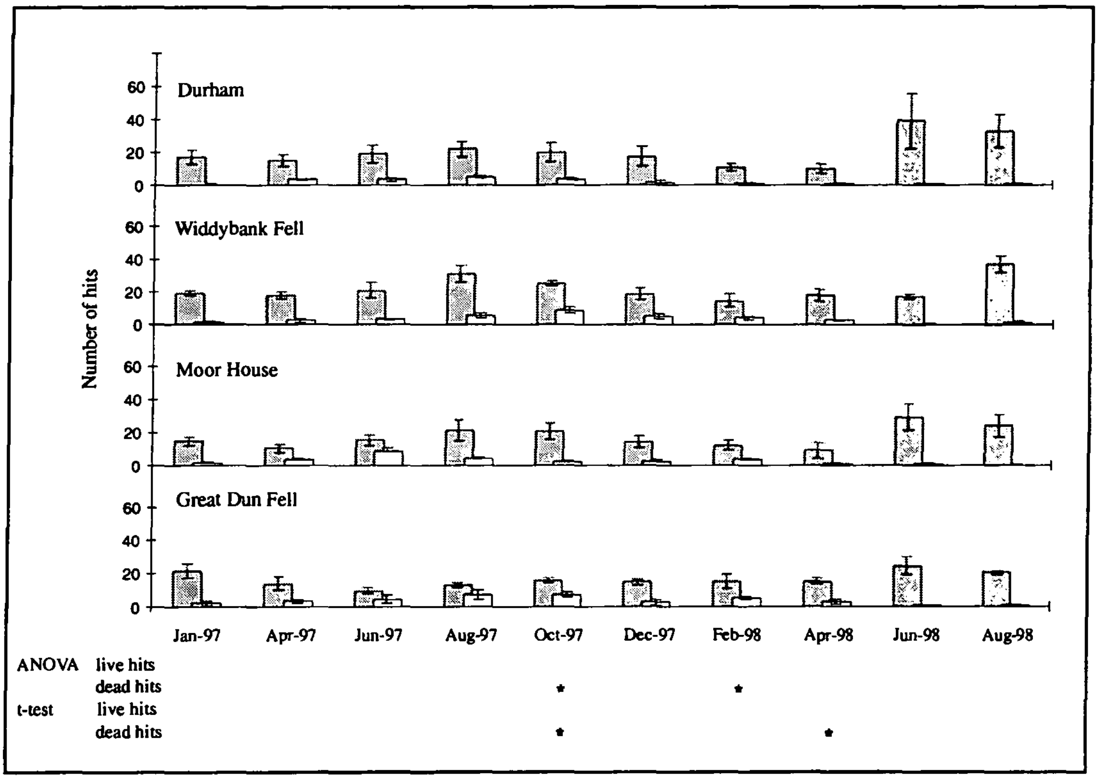



**Figure 7.8** ***Thymus praecox*** **subsp.** ***arcticus*** **- Nodum 21 & 4 microcosms.**

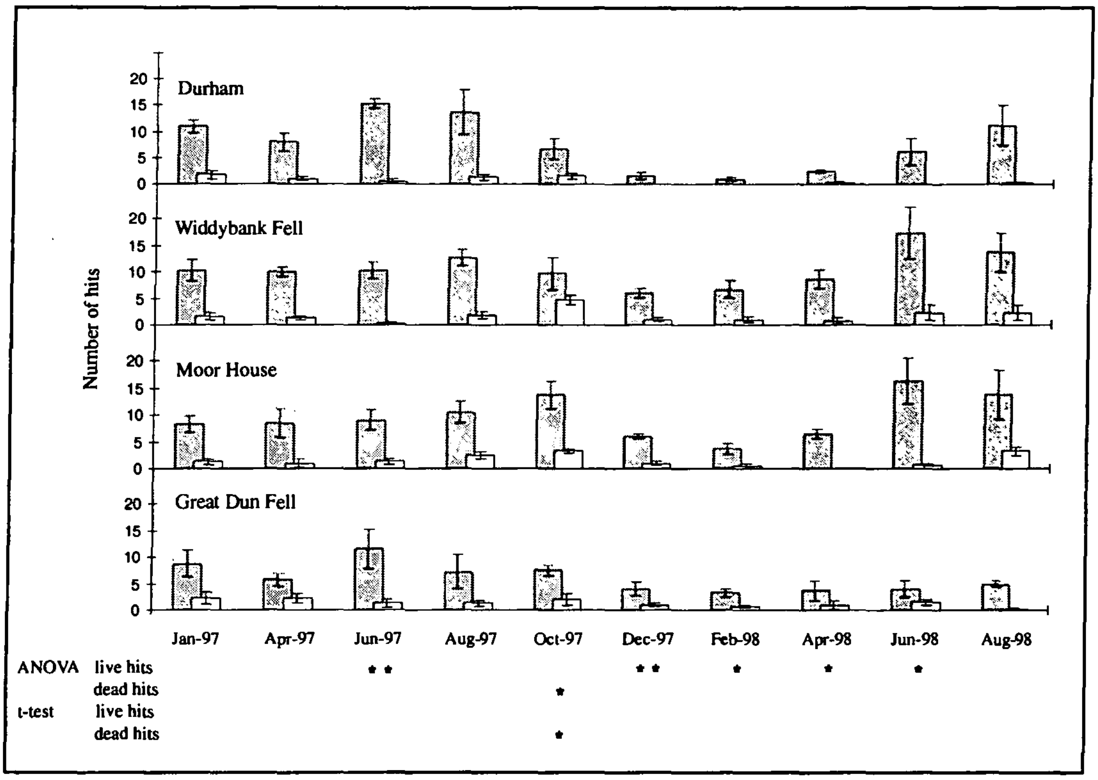



**Figure 7.9** ***Trifolium repens*** **- Nodum 33 microcosms.**

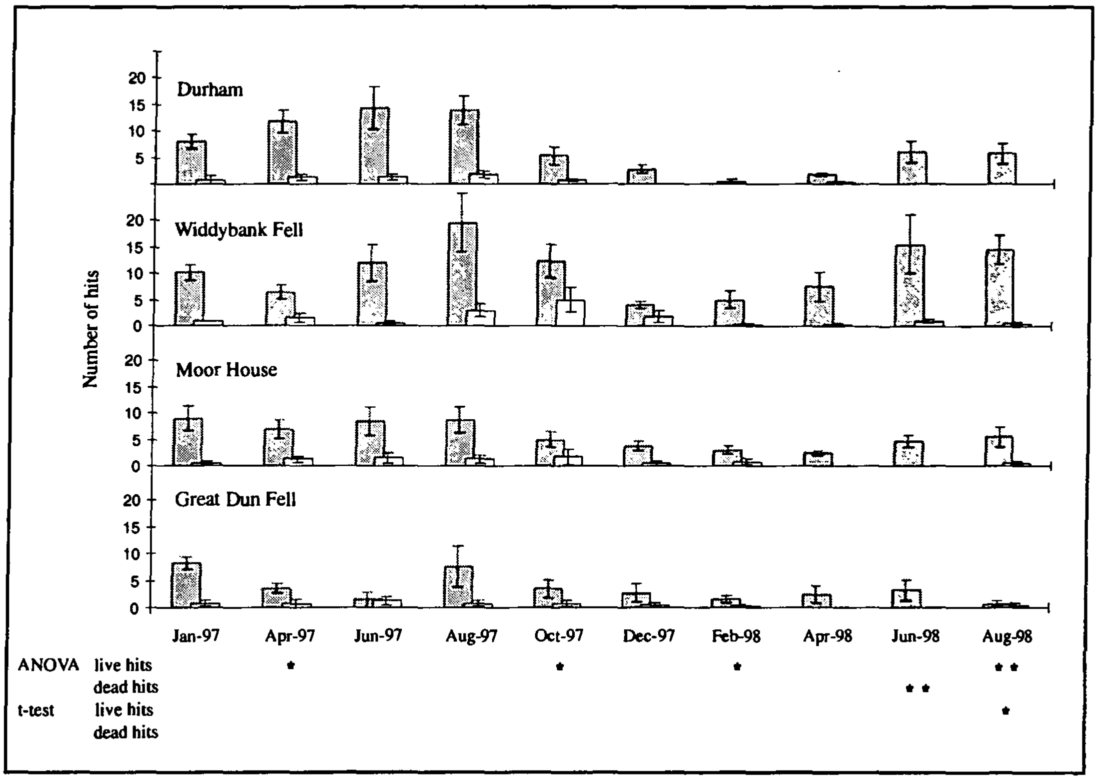



**Figure 7.10** ***Trifolium repens*** **- Nodum 21 &4 microcosms.**

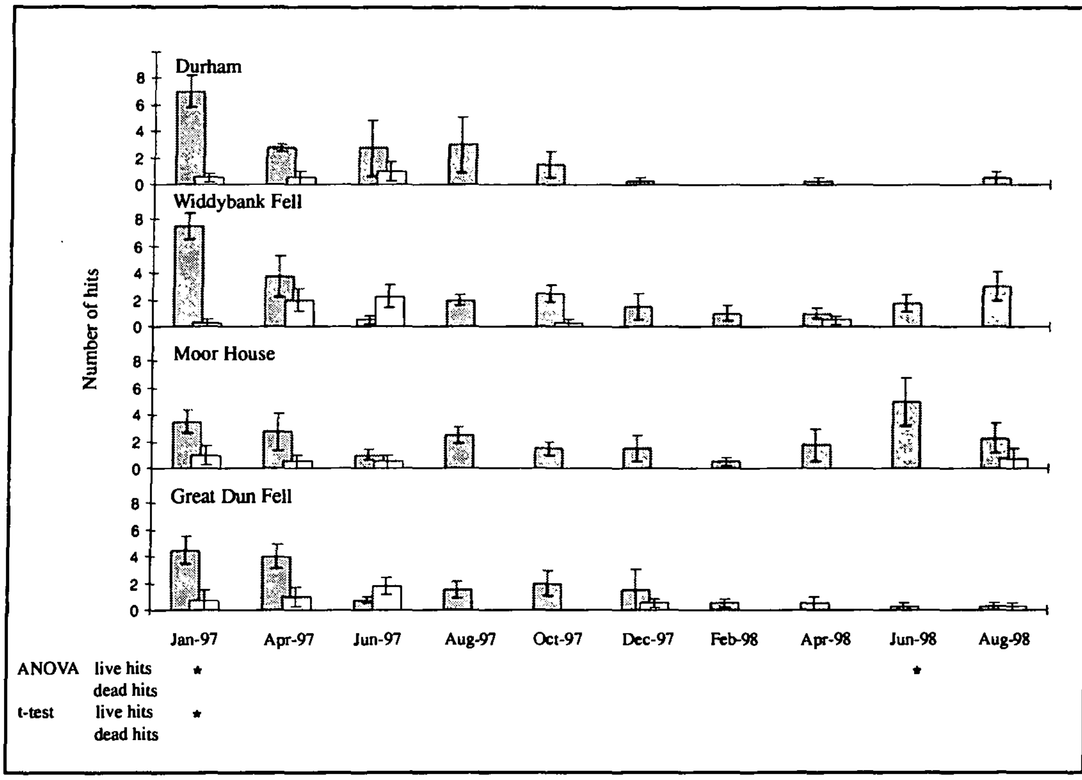



**Figure 7.11** ***Viola lutea*** **- Nodum 33 microcosms.**

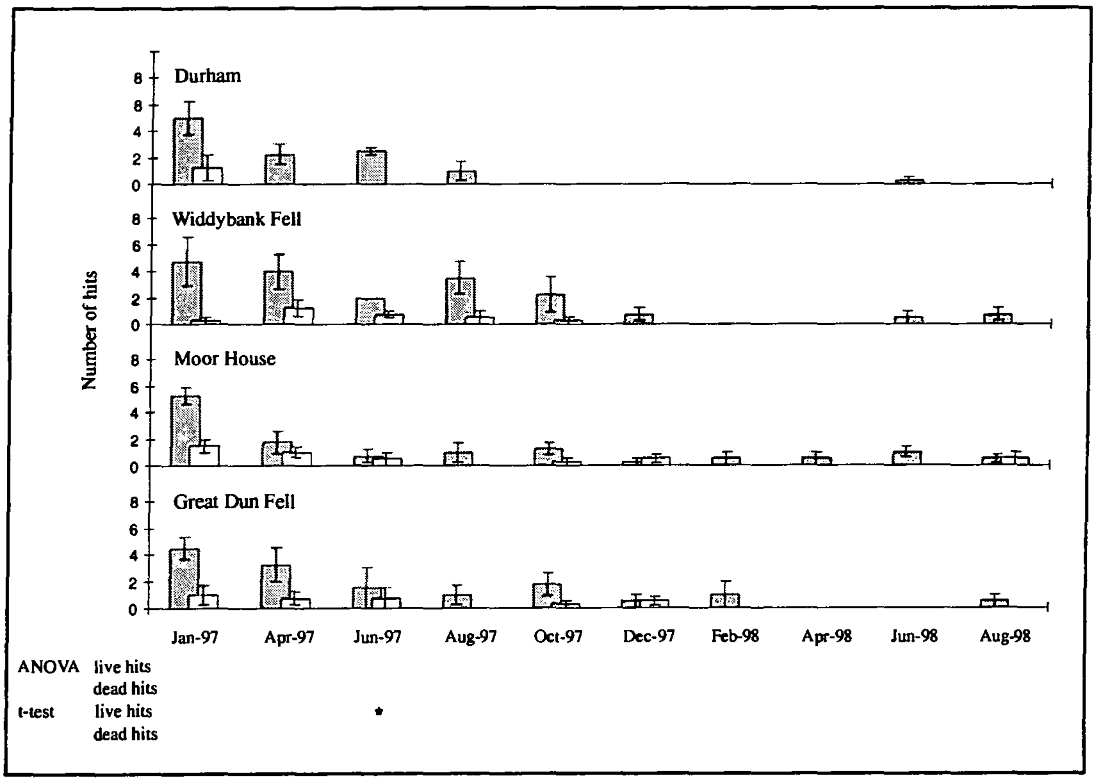



**Figure 7.12** ***Viola lutea*** **- Nodum 21 & 4 microcosms.**

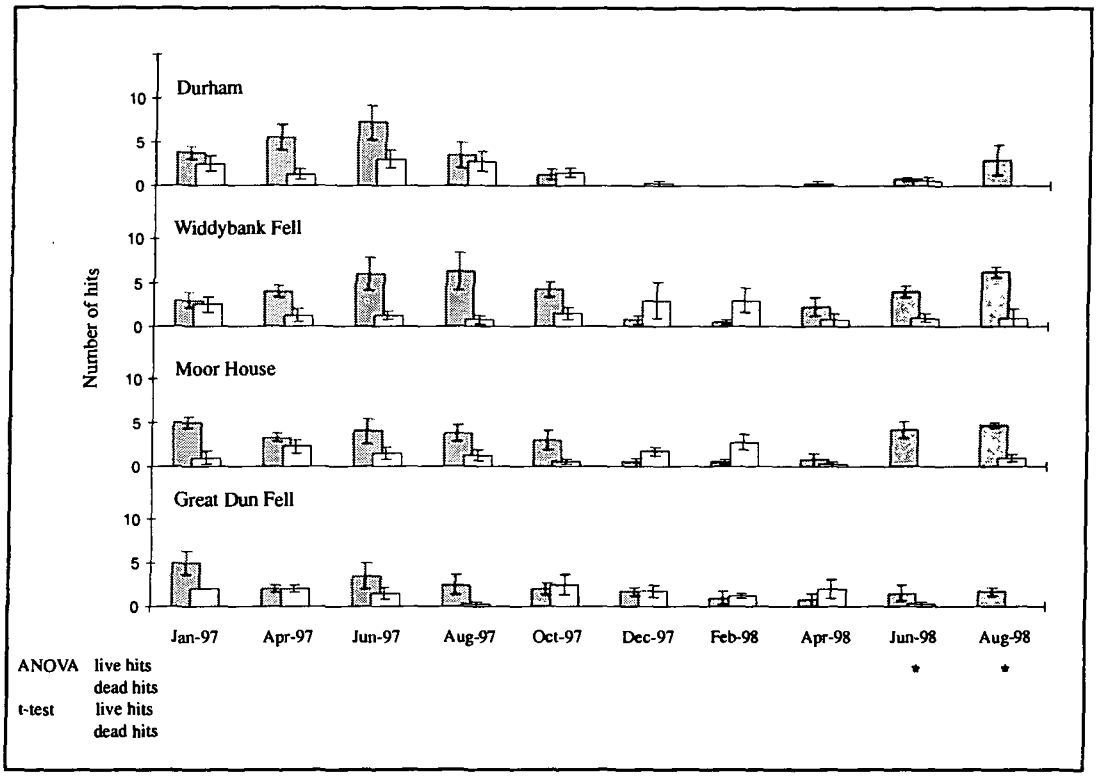



**Figure 7.13** ***Achillea millefolium*** **- Nodum 33 microcosms.**

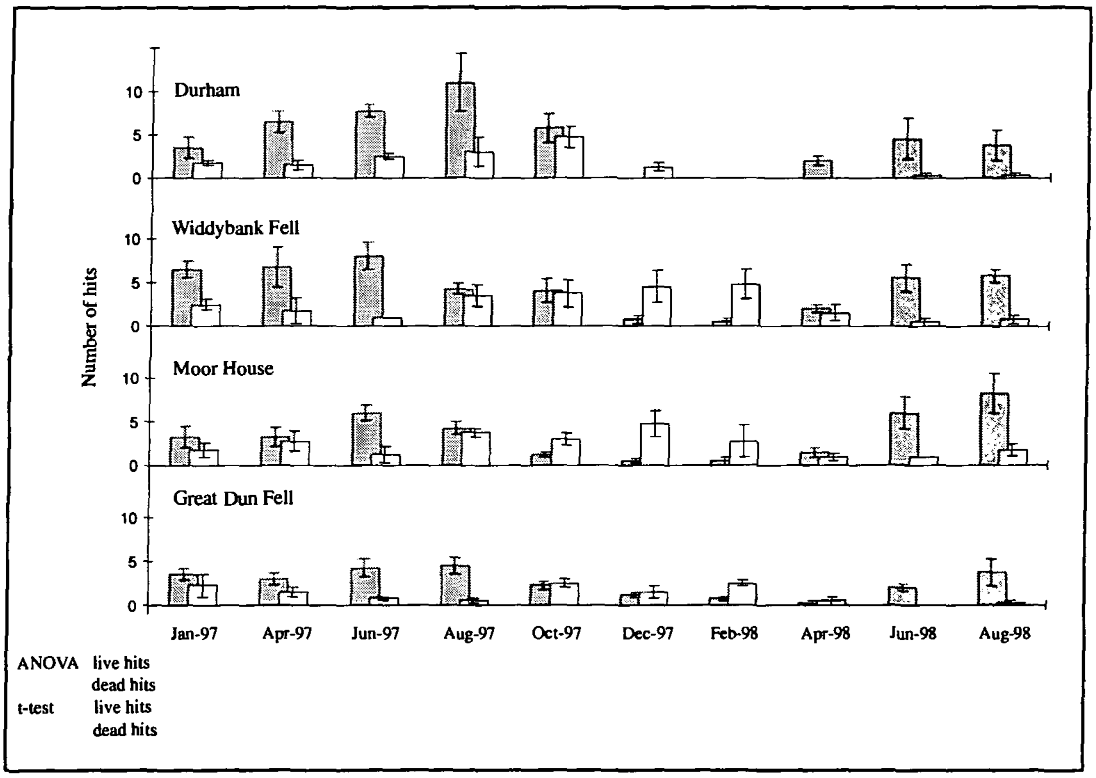



**Figure 7.14** ***Achillea millefolium*** **- Nodum 21 & 4 microcosms.**

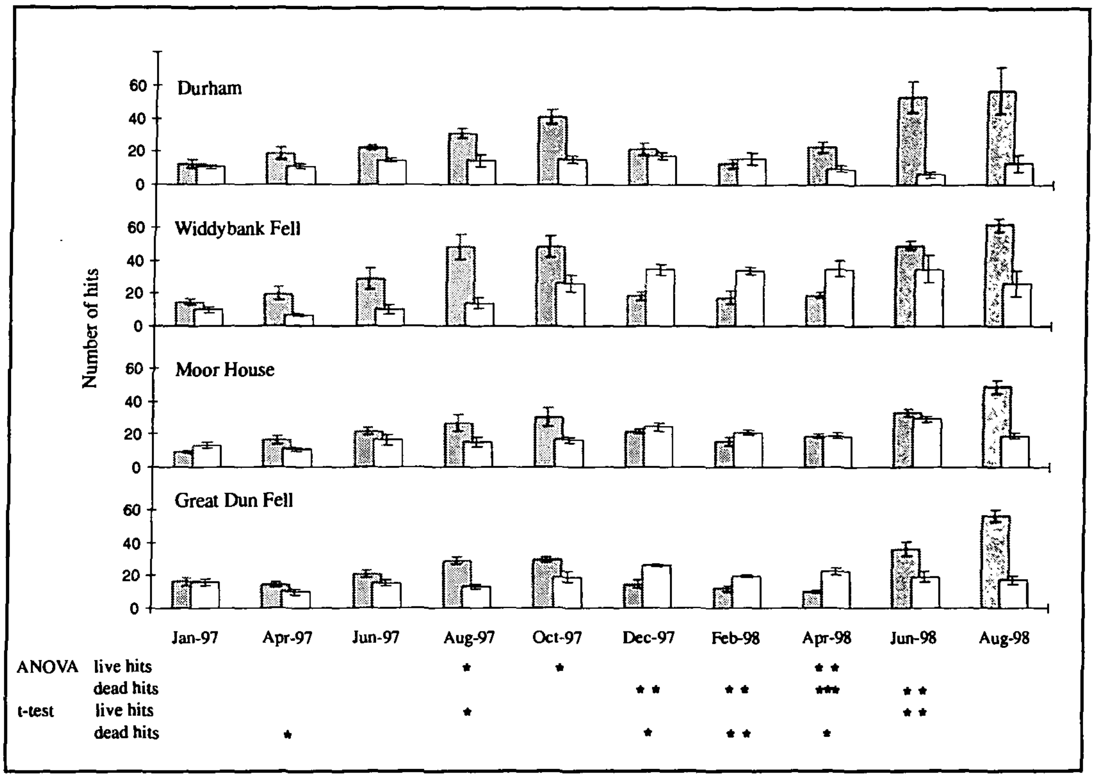



**Figure 7.15** ***Sesleria albicans*** **- Nodum 21 & 4 microcosms.**

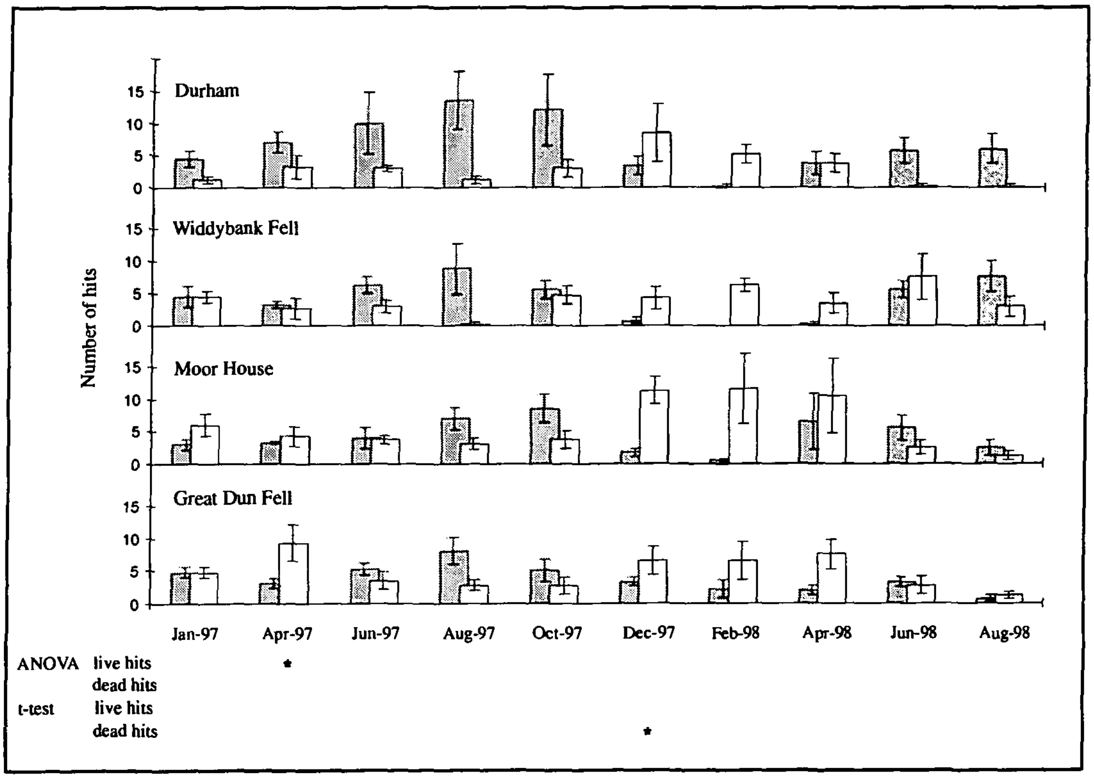



**Figure 7.16** ***Agrostis vinealis*** **- Nodum 21 & 4 microcosms.**

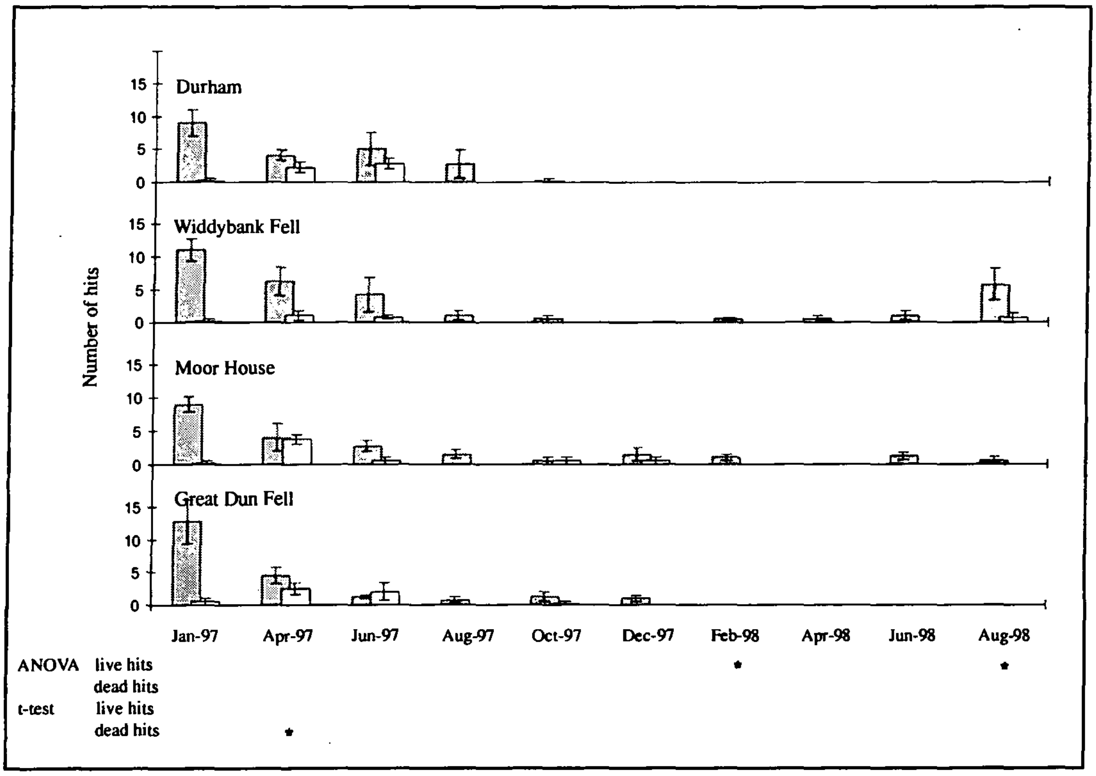



**Figure 7.17** ***Galium saxatile*** **- Nodum 33 microcosms.**

For *Festuca ovina* in both microcosm types (Figures 7.5 & 7.6) mean number of live hits were at their peak in both summer periods, producing a clear bimodal distribution. There was a significant difference in number of live hits between the four sites on around half the sampling dates, mainly during the summer period in both seasons, with some months also significant at the multiple probability level. The differences in number of hits corresponded to the altitudinal gradient, with more hits at Durham, intermediate at Widdybank and Moor House and less at Great Dun Fell. The differences between sites became more pronounced after two seasons, which probably reflected the underlying trend of increase in number of hits. A seasonal lag between sites is also noticeable, with peak hits for 1997 being reached in August for Durham, Widdybank and Moor House but not until October at Great Dun Fell, and a similar pattern observed in 1998. Significant differences in number of dead hits between the four sites were also seen, a reflection of the differences in live hits between sites. Despite the strong differences across the four-site transect, there were fewer dates when there was a significant difference between Widdybank and Moor House for either live or dead hits and none were significant at the multiple probability level.

For *Thymus praecox* subsp. *arcticus* (Figures 7.7 & 7.8) there was no significant difference for live hits on any sampling date between the four sites in either microcosm type. Mean number of hits was remarkably consistent across the sites and dates, with no noticeable increase above the number of hits recorded in the baseline survey (of the newly planted microcosms, in January 1997) until June 1998; but even then differences in growth performance were not significant between sites. There were differences in number of dead hits on a few sampling dates, but with no consistent pattern emerging.

For *Trifolium repens* (Figures 7.9 & 7.10) as seen for *Festuca*, a bimodal distribution of live hits reflecting seasonal growth patterns was observed in both microcosm types, but only for Nodum 33 microcosms at Widdybank and Moor House was the mean number of live hits greater in the second season than the first. The effects of the altitudinal gradient were also less clear. In the Nodum 33 microcosm the four sites only differed significantly in live hits on one occasion in the first season. In the second season however, plants at Widdybank and Moor House were growing significantly better than those at Durham or Great Dun Fell. In the Nodum 21 & 4 microcosms, performance at Widdybank was generally better than at the other three sites for both seasons, with a significant difference between sites for live hits on four occasions, although not at the stringent multiple probability level.

*Viola lutea* (Figures 7.11 & 7.12) showed a rapid decline in abundance over the first growing season and with one exception, no recovery above the baseline number of live hits. In the second season of growth in the Nodum 33 microcosms, performance was noticeably better at Widdybank and Moor House than at the other two sites; this difference reached the level of significance in June 1998. In the Nodum 21 & 4 microcosms *Viola* has persisted at apparently low density at all sites, although for the Nodum 21 & 4 microcosms at Durham there was only one record between October 1997 and August 1998.

*Achillea millefolium* (Figures 7.13 & 7.14) showed a clear seasonality in number of live hits (i.e. the bimodal distribution with summer peaks) but no significant difference between sites for any date in the Nodum 21 & 4 microcosms. In the Nodum 33 microcosms there was a significant difference between the four sites for live hits only in the summer of 1998 when Widdybank and Moor House had a greater number of hits than the other two sites.

*Sesleria albicans* (Figure 7.15, present in the Nodum 21 & 4 microcosms only) showed clear seasonality in number of live hits, as previously seen for other species, and a significant difference between the four sites for live hits on three occasions and for dead hits on four occasions (once at the multiple probability level). The best overall growth performance was seen at Widdybank.

*Agrostis vinealis* (Figure 7.16, planted in the Nodum 21 & 4 microcosms only) only showed a significant difference in number of hits between sites on two occasions, no more than expected by chance alone. Overall performance in the first year was better than seen in the second.

*Galium saxatile* (Figure 7.17, Nodum 33 microcosms only) showed a similar growth trend to *Viola*, one of consistent decline in the microcosms, and was not recorded at Durham after October 1997 or at Great Dun Fell after December 1997. Populations remained apparently stable at Widdybank and Moor House in 1998, but at only a fraction of the number of hits recorded in the baseline survey (in January 1997). The only dates for which there was a significant difference between sites was for live hits in February and August 1998 between the four sites i.e. after *Galium* had apparently died out at two sites.

### 7.3.2 *Relative performance between sites for each species over the entire experimental period*

Figures 7.18-7.25 show mean total hits for all sampling dates combined for each species in the two microcosm types. Results from ANOVAs and t-tests examining inter-site differences are also given, in Table 7.4. Multiple probability was again calculated; for the 13 tests performed the equivalent of $P \leq 0.05$ for an individual test is modified to $P \leq 0.0039$ (approximately).

There were significant differences in performance between the four sites for three species. *Festuca* in both microcosm types had a significant difference between sites for both live and dead hits and apart from dead hits in the Nodum 21 & 4 microcosms, all tests for *Festuca* were significant at the multiple probability level. As previously observed for individual dates, the overall pattern was of the most hits at Durham and the least at Great Dun Fell, accurately reflecting the altitudinal gradient. *Trifolium*, in the Nodum 33 microcosms only, had a significant difference in number of live hits, with the greatest number of hits at Widdybank. *Sesleria* had a significant difference in number of dead hits between the four sites, with the most hits again at Widdybank.

**Figures 7.18-7.23 Mean total live (filled bars) and dead (empty bars) point quadrat hits on each species in the two microcosm types for all sampling dates combined (i.e. per 1000 pins). Note the differences in scaling of the y-axis between species.**

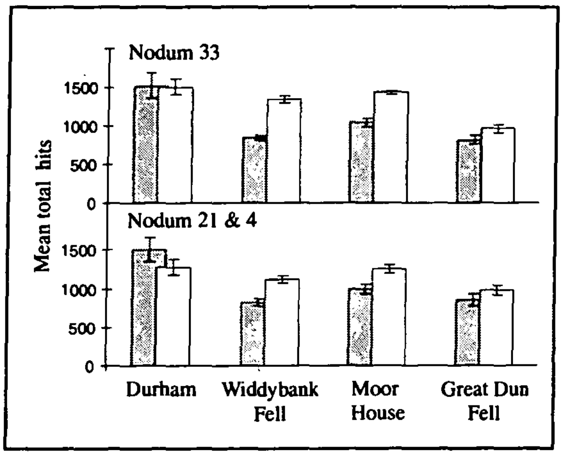



Figure 7.18 *Festuca ovina.*

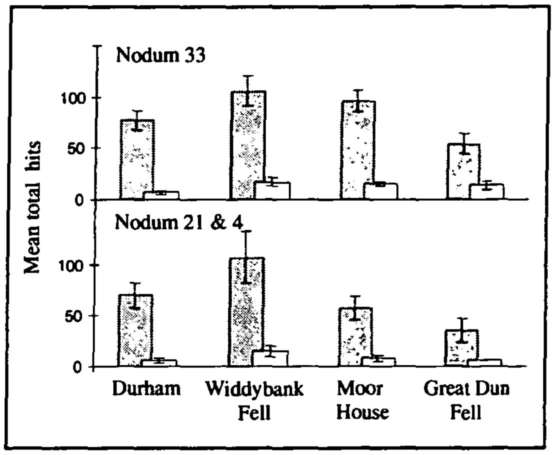



Figure 7.19 *Trifolium repens.*

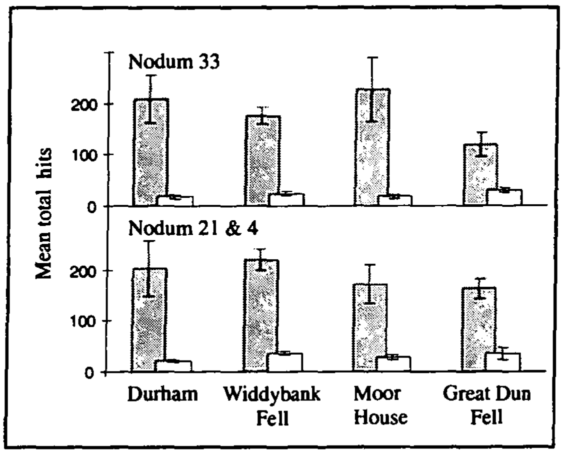



Figure 7.20 *Thymus praecox* subsp. *arcticus.*

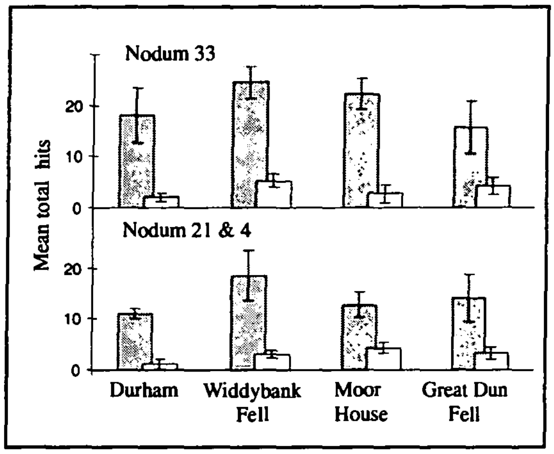



Figure 7.21 *Viola lutea.*

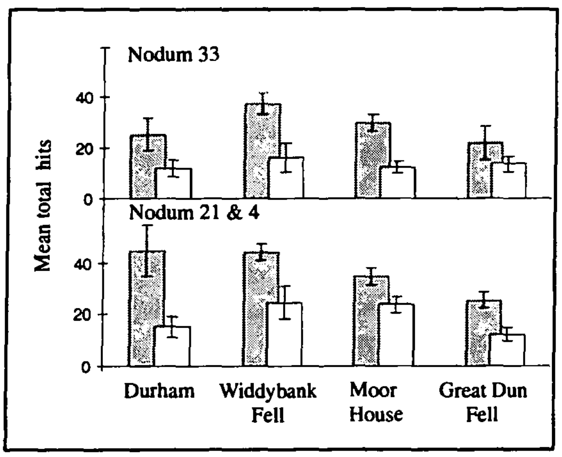



Figure 7.22 *Achillea millefolium.*

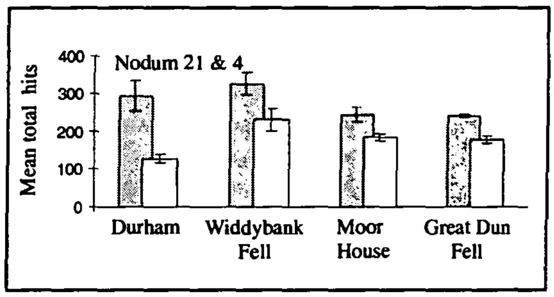



Figure 7.23 *Sesleria albicans.*

**Figures 7.24 & 7.25 Mean total live and dead hits for all sampling dates continued..**

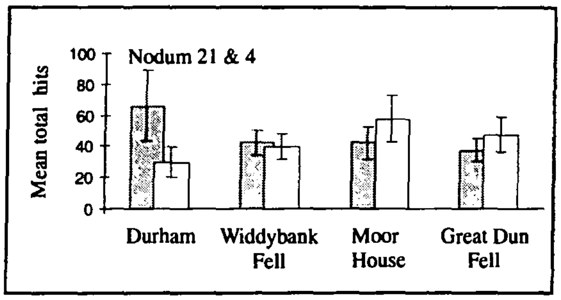



**Figure 7.24** ***Agrostis vinealis.***

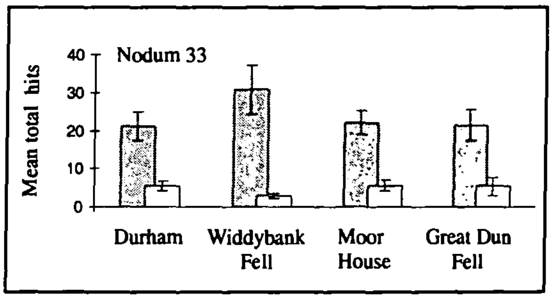



**Figure 7.25** ***Galium saxatile.***

**Table 7.4 Significant differences between number of total hits for the four sites (examined using ANOVA) and between Widdybank Fell and Moor House (examined using t-tests) for each species and microcosm type (* P≤ 0.05, ** P≤ 0.01, *** P≤ 0.05 at the multiple probability level).**

| | | *Festuca ovina* | | *Trifolium repens* | | *Thymus praecox* | | *Viola lutea* | | *Achillea millefolium* | | *Sesleria albicans* | *Agrostis vinealis* | *Galium saxatile* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 33 | 21 & 4 | 33 | 21 & 4 | 33 | 21 & 4 | 33 | 21 & 4 | 33 | 21 & 4 | 21 & 4 | 21 & 4 | 33 |
| ANOVA | live hits | *** | *** | * | | | | | | | | | | |
| | dead hits | *** | * | | | | | | | | | * | | |
| t-test | live hits | * | | | | | | | | | | | | |
| | dead hits | | | | | | | | | | | | | |

Between Widdybank and Moor House there was a significant difference only for one species and microcosm type: live hits on *Festuca* in the Nodum 33 microcosm, with a greater number of hits at Moor House. However, this did not reach the level of significance in multiple probability.

### *7.3.3 Relative performance between sites for the whole community*

Figures 7.26 & 7.27 show total number of hits for all species, representing overall community performance in the Nodum 33 and Nodum 21 & 4 microcosms, respectively, in the four sites with results from ANOVAs and t-tests given in Table 7.5. As seen for many of the individual species, overall performance follows the altitudinal gradient, with the highest number of hits at Durham and the lowest at Great Dun Fell, with an intermediate number of hits for Widdybank and Moor House. Differences between the four sites were significant for both live and dead hits in the two microcosm types. Differences between Widdybank and Moor House were significant only for live hits in the Nodum 33 microcosms, with more hits at Moor House, however for the Nodum 21 & 4 microcosms, the opposite was true and there were marginally more hits at Widdybank.

### *7.3.4 Species performance between the Nodum 33 and Nodum 21 & 4 microcosms*

The results from the comparison of species performance between the two microcosm types are given in Table 7.6. (Figures 7.18-7.25 represent the data used for this analysis, but without any correction for initial differences in number of species planted in the two microcosm types). *Achillea* had significantly more live and dead hits in the Nodum 21 & 4 than the Nodum 33 microcosms at Moor House. *Festuca* had significantly more dead hits in the Nodum 21 & 4 than the Nodum 33 microcosms at Great Dun Fell. None of these were significant at the multiple probability level.

**Figures 7.26 & 7.27 Mean number of hits (per 1000 pins) for all species combined in the Nodum 33 and Nodum 21 & 4 microcosms at the four sites.**

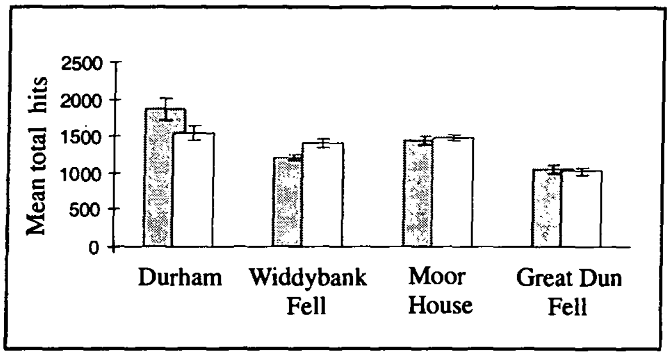



**Figure 7.26 Nodum 33 microcosms.**

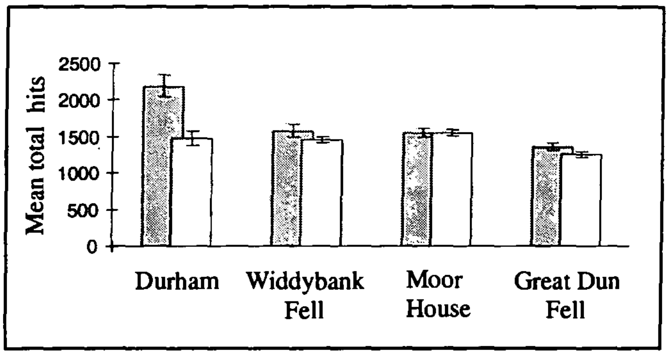



**Figure 7.27 Nodum 21 & 4 microcosms.**

**Table 7.5 Significant differences between number of total hits for all species the four sites (examined using ANOVA) and between Widdybank Fell and Moor House (examined using t-tests) for each microcosm type. (* P ≤ 0.05 ** P ≤ 0.01).**

| | | Nodum 33 microcosms | Nodum 21 & 4 microcosms |
|---|---|---|---|
| ANOVA | live hits | ** | ** |
| | dead hits | ** | * |
| t-test | live hits | * | |
| | dead hits | | |

**Table 7.6 Significant differences in number of hits between the Nodum 33 and Nodum 21 & 4 microcosms for the five species occurring in both microcosm types (* P$\leq$ 0.05 ** P$\leq$ 0.01). (Calculated after adjustment for differences in initial number planted between the two microcosm types were made - see text). D= Durham, W= Widdybank Fell, M= Moor House, G= Great Dun Fell.**

| | | *Festuca ovina* | | | | *Trifolium repens* | | | | *Thymus praecox* | | | | *Viola lutea* | | | | *Achillea millefolium* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | D | W | M | G | D | W | M | G | D | W | M | G | D | W | M | G | D | W | M | G |
| t-test | live hits | | | | | | | | | | | | | | | | | | | * | |
| | dead hits | | | | * | | | | | | | | | | | | | | | ** | |

### *7.4 Discussion*

The null hypothesis of no significant difference in species performance between the four sites is rejected. At the three levels of investigation, testing for differences in:

1. Species performance (i.e. number of hits) at the four sites on individual sampling dates
2. Overall species performance (total hits) over the experimental period
3. Overall community performance (for all species combined) over the experimental period

there were significant differences between the four sites for both live and dead hits.

The differences in plant performance between sites were clearly related predominantly to the prevailing temperature. Plant productivity generally decreased with altitude; this reflected the reduced temperature sum (see Table 7.3). The difference in the length of growing season between the sites was also apparent, for example for *Festuca* in 1997 where Durham, Widdybank and Moor House had the greatest number of hits in August, whereas the *Festuca* at Great Dun Fell lagged behind, reaching peak productivity in October. Other climatic differences between sites may have been of some importance. On Great Dun Fell in particular, as well as having a cooler climate, the higher windspeeds may also have depressed plant production. When exposed to high winds, plants tend to partition resources into structural components and are shorter and more stocky than equivalent plants in sheltered areas (Salisbury & Ross, 1992). In Durham, plant growth was more likely to have been limited by water stress than at the other sites as it received the least rainfall, but productivity for most species in the Durham microcosms was still much higher than at the upland sites.

It is interesting that despite the significant differences for four sites comprising the altitudinal transect there were fewer differences in species performance between microcosms in the two-site investigation, between Widdybank and Moor House. This would be expected to some extent, because the temperature difference between the two sites was less extreme. The lack of difference in growth performance between these two sites could also result from the relatively short experimental period; one justification for continuing to monitor the microcosms in the future. Long-term responses of the microcosms to relatively subtle temperature differences are clearly of interest.

Although fewer of the tests on total hits over the two growing seasons were significant, such tests don't take into account periods of winter dormancy (e.g. when mean temperatures fall below 5.5 °C *sensu* Manley, 1968) when there may be no difference in species growth for several months.

The null hypothesis of no difference in species performance between Nodum 33 and Nodum 21 & 4 microcosms is accepted, as the number of t-tests significant were only about that expected by chance alone. As well as no effect of soil type on growth, the different companion species and sward density (note the more open sward in the Nodum 33 microcosms, Plates 7.3 (a) & (b) and Plate 7.4 (a) & (b)) also apparently made no difference to species performance. It is also interesting to note that the apparent differences in original rooting success in the *Viola* and *Achillea* plants between the two microcosm types were also not reflected in these results. The lack of difference in species performance in the two microcosm types could perhaps be explained by the relatively minor differences in initial soil pH (6.78 in the Nodum 33 microcosms and 6.95 in the Nodum 21 & 4 microcosms). Alternatively, two seasons may be an insufficient length of time for these differences in soil pH (or other soil characteristics) to be reflected in the vegetation.

The remainder of the discussion examines the performance of the individual species and, where appropriate, compares their growth response in the microcosm with any observed changes in abundance measured *in situ* on Widdybank Fell.

*Festuca ovina* and *Sesleria albicans* (Nodum 21 & 4 microcosm only) can be described as "winners" in terms of in the first summer, producing a general increase in number of live hits compared to their original scores in January 1997. Additionally, scores in the second summer were often greater than those seen in the first. This consistent increase in number of hits was generally true for all sites.

*Festuca* had the greatest increase in number of hits (compared to baseline) for any species, and also exhibited clear differences in growth response between sites. Despite this evident climatic sensitivity, *Festuca* was not found to have changed in abundance compared to the survey of Jones (1973) in any of the three noda comprising the microcosms, either by the survey of Willis (1995) or the present survey. This is probably because in mature, closed communities it has less opportunity to respond to climate change by extending through tillering, and because in such communities it is usually subject to some grazing pressure.

*Sesleria* (present in the Nodum 21 & 4 microcosm only) showed a similar growth response to *Festuca* in terms of a cumulative increase in number of hits compared to baseline levels over the two seasons. It is also a relatively competitive species in communities composed mainly of other stress-tolerators, with a wide ecological tolerance, for example withstanding a temperature range from -25°C to 40°C (Dixon, 1996). It produces a considerable litter layer, which may conceivably aid in the suppression of potential competitors. Unlike *Festuca* there was not such a clear difference in performance between the four sites. There was no recorded change in abundance for *Sesleria* in Nodum 21 between the survey of Jones (1973) and either the survey of Willis (1995) or the present survey. (See Table 3.3 for a summary of species changes found by the present survey). The lack of apparent sensitivity to different climatic conditions in the microcosms hence fits with these findings.

*Thymus praecox* subsp. *arcticus, Trifolium repens, Achillea millefolium* and *Agrostis vinealis* maintained a relatively consistent presence in the microcosms over the experimental period.

*Thymus* showed the least change in abundance over the two experimental seasons, and the least difference in growth response between sites. It is a slow growing, evergreen stress-tolerator with leaves generally surviving for more than one season (Grime et al., 1988). As such it could have been predicted to show a conservative response to climate change. However *Thymus* was found to have significantly changed in abundance both by the present survey and by Willis (1995). Hence there is clear value in continuing to monitor the microcosms to follow the success of *Thymus* beyond the duration of this project. Fraser and Keddy (1997) note that microcosm studies of up to five years may be necessary for slow growing perennial plants.

For *Achillea* in both microcosm types, the lack of any significant difference in growth response between sites is perhaps surprising. *Achillea* was newly recorded in Nodum 33 in both the survey of Willis (1995) and the present survey, reaching the level of significance in the former (compared to the survey of Jones 1973). *Achillea* is also known to demonstrate considerable plasticity in growth response and can be found over a wide part of the northern hemisphere (Warwick & Black, 1982). The relatively poor performance in the second season compared to the first may imply that *Achillea* is losing out to the competitive effects of its neighbours. It is known to be relatively intolerant of competition against larger herbs (Grime et al., 1988).

*Trifolium* was also apparently losing out to more competitive neighbours at Durham with a poorer growth performance in the second year. It is shade-intolerant (Grime et al., 1988) and was probably being affected to some extent by the taller grasses at this site. Intolerance of severe frosts (Burdon, 1983) may have been one factor contributing to the poor growth at Great Dun Fell. *Trifolium* was not found to have changed in abundance in Nodum 33 at Widdybank by either of the two recent surveys, and the present survey recorded no change in Nodum 21 either, (although Willis (1995) found evidence for a decrease in abundance). Hence the lack of difference in growth response between Widdybank and Moor House is not surprising.

*Agrostis* also grew less well in its second season. It has a limited capacity for vegetative expansion (Grime et al., 1988) and hence may have been at a disadvantage compared to other grasses in the microcosm, such as *Festuca.* There was no difference in performance between sites, again perhaps surprising as it was newly recorded in Nodum 4 by both the survey of Willis (1995) and the present survey (reaching the level of significance compared to the survey of Jones (1973) in the latter).

The two obvious "losers" in the microcosms were *Viola lutea* and *Galium saxatile.* Their decline in abundance was consistent across the sites and was probably due to the generally poor rooting success of the collected plants and their consequent mortality in the spring frosts. It was unlikely to be the consequence of any competitive effects so early on in the experiment, when there was still a certain amount of uncolonised ground between individual plants. In fact, the existence of this relatively open sward may have been in itself unfavourable to *Viola* and *Galium.* Field transplant and greenhouse experiments on *Viola* have demonstrated that the species is susceptible to drought, and it is limited in range by its requirement for high humidity throughout the year (Balme, 1954). The poor survivorship in the second season at Durham may be for this reason. *Galium* is generally associated with North-facing slopes (Grime et al., 1988) suggesting intolerance to drought, and population fluctuations in Breckland have been shown to correspond to seasonal variation in rainfall (Watt, 1960). Another factor which may have been unfavourable to *Galium* was the use of homogenised soil in the microcosms. As a calcifuge, *Galium* may have grown successfully *in situ* because of the potential for it to root in the relatively base-leached upper parts of the soil profile. Further investigation of the soil characteristics of Nodum 33 would hence be of interest.

## *7.5 Conclusions*

The species in the microcosms have shown different growth responses in the different temperature regimes represented by the four sites along the altitudinal gradient. Despite this evidence for temperature sensitivity of some of the species it is interesting that there is little correspondence between the species that have been shown from this study to be the most temperature sensitive with those showing greatest evidence of vegetation change on Widdybank Fell.

Excluding *Viola lutea* and *Galium saxatile*, out of the six remaining species present in the microcosms, only two had growth responses that could have been predicted based on the records of vegetation change from Widdybank. Equally the lack of overall difference in species performance between the two microcosm types was surprising, compared to the obvious differences between noda from the vegetation surveys on the fell. The data presented here were obtained in the early stages of microcosm establishment, so it is possible that further differences in species performance between sites may emerge as the communities in the microcosms continue to mature. Microcosm monitoring is ongoing, currently with an annual survey each August.

In the future, it would be desirable to fully characterise the soils in the two microcosm types, for example examining differences in cation exchange capacity, loss on ignition and in organic and inorganic nitrogen and phosphorus content. If these soil characteristics proved similar, one option might be to pool the results from the surveys of the two different microcosm types for the species common to both. It would also be interesting to compare characteristics of the homogenised soil with the potentially different properties of the different soil profiles *in situ* (as described above, the performance of *Galium saxatile* in the Nodum 33 microcosms could have been adversely affected by soil homogenisation).

Another potential use for the microcosms could be to examine their response to nitrogen and phosphorus fertilisation. Some of the grasslands on the sugar limestone soils are phosphorus-limited; it would be interesting to observe if the same was true for other grassland types on Widdybank Fell. For such an experiment it might be more desirable to use intact turf and soil monoliths, in order to avoid disturbance to the soil profile. It is possible, however, that temperature is the strongest limiting factor for the microcosms and that the soils used are reasonably well provisioned with nutrients. The increased growth in the microcosms at Durham compared to the upland sites could infer this, although clearly rates of soil mineralisation will also increase with temperature.

The advantages of this type of microcosm experiment are that it maintains a reasonable amount of realism in using an outdoor environment as opposed to a growth room, a growth medium based on real soil and a mixture of different species in naturally-occurring proportions. There is clearly some loss of realism in the limited number of species used in the microcosm and in the use of homogenised soil (together with commercially obtained substrates) but this method does have the advantage of easily creating replicates. In terms of setting up the microcosms, it would have been desirable to allow longer for the propagation stage, particularly given the difficulty some species showed in rooting after collection. If time constraints had not been so severe it would also have been better to establish the microcosms along the altitudinal transect during the summer months, when the transfer from the propagation site at Durham would have been less of a shock to the plants- the January start to the experiment was not ideal. A disadvantage of the use of the altitudinal transect was the confounding climatic variables. Clearly the Durham site receives significantly less rainfall than the others and now that the differences in precipitation have been characterised, there could be a case for supplementary watering of the microcosms at Durham.

### *7.6 Summary*


- This chapter investigated the temperature sensitivity of selected species and vegetation types on Widdybank Fell. This was achieved through the use of a microcosm experiment. The experiment used two grasslands types, Nodum 33 and Nodum 21 & 4, from Widdybank placed along an altitudinal gradient that consisted of four sites: Widdybank Fell (513 m with an impounded catchment), the nearby Moor House (560 m, an unimpounded catchment), Durham (102 m) and Great Dun Fell (847 m). Species performance was monitored using a point quadrat.

- The major null hypothesis tested was that the species were insensitive to temperature and thus would grow equally well at all four sites. Additionally it was hypothesised that species common to the two grassland types would perform equally well in both soil types.

- The null hypothesis of no difference in species performance between the four sites was rejected, as with few exceptions there was a clear temperature response in terms of species growth between sites that followed the altitudinal gradient i.e. the best performance generally at Durham and the poorest at Great Dun Fell. However there was no significant difference overall in species performance between Widdybank and Moor House; neither was there evidence of difference in performance between the two microcosm types (Nodum 33 and Nodum 21 & 4) in species common to both.

- Of the species selected for the study there was generally poor correspondence between observed performance and that which might have been predicted using the evidence for vegetation change *in situ* on Widdybank Fell.

# 8. Discussion

## 8.1 Introduction

This chapter considers the impact of the construction of Cow Green Reservoir on the vegetation of Widdybank Fell. The implications for future management and conservation of the plant communities and specifically the Teesdale "rarities" on Widdybank Fell are also discussed. Finally the threat of global warming is considered with relation to the local impacts of Cow Green Reservoir as a potential model for climate change.

## 8.2 Climate change factors and their relative importance in explaining the vegetation changes

What have been the impacts of the construction of Cow Green Reservoir? Evidence that the reservoir has produced a modification of the local climate is given in Chapter 5. Can the demonstrated "lake effect" account for the observed changes in the vegetation of Widdybank Fell? A number of specific changes in the vegetation would have been expected as a response to a lake effect-modified climate. These included:

- A loss of species in geographic range categories that cover cold regions (e.g. species in the Arctic-montane major biome category (Preston & Hill, 1997). Species with their ranges centred on cold regions, especially those with Teesdale as their southern British geographical (and hence potentially climatic) limit, might be expected to find climatic amelioration particularly deleterious.

- An increase in species relying on seed production as their reproductive strategy, favoured by the warmer mean temperatures in autumn, with a greater potential for successful seed set.

- An increase in species with a large nuclear DNA content, able to respond favourably to the relatively cooler mean temperatures in spring.

None of these species or species groups had changed in abundance any more than the flora as a whole.

There was only one change that might have been predicted, based on the observed effects of the reservoir on the local climate. This was the significant reduction in the number of stress-tolerator species. Although this is interesting, it does not provide direct evidence of a response to a "lake effect" modified climate because there are a number of other environmental stresses that also may have decreased. For example, nutrient stress at Widdybank may have been ameliorated (for some species on some soils) as a result of the increased levels of atmospheric nitrogen deposition.

Two studies of the vegetation of the fell have failed to detect any differences in the vegetation with distance from the reservoir margin. The analysis described in Chapter 5 of the vegetation relevés based on their distances from the reservoir detected no significant difference in species composition. The point quadrat study by Maxwell (1997) along a transect in Nodum 4 (limestone heath) also showed very few differences in species composition with distance from the reservoir.

The results from the microcosm experiment in Chapter 7 indicate that the species used *are* temperature sensitive when exposed to the most "extreme" climates along the altitudinal gradient. However the minor temperature differences between Widdybank Fell and Moor House were apparently not sufficient, at least in the short term, to produce a differential growth response in the microcosms. The communities in the microcosm experiment were still in their establishment phase, so longer-term results from this study will be of interest. At present, however, this experiment also fails to provide evidence for the importance of the "lake effect" in accounting for the changes in the vegetation of the fell.

Hence overall there is very little evidence directly linking the changes in the vegetation to the presence of the reservoir. There are three reasons why there may be so little apparent response by the vegetation to the reservoir:

1. The climatic changes produced by the "lake effect" are not of sufficient magnitude to be of biological significance. This was discussed in Chapter 5 and it was concluded that the changes were of potential significance, particularly the moderation of minima at ground (and hence plant) level.

2. The changes are important, but are ongoing; the vegetation is still in the process of equilibrating to them, so the full effects have not yet been seen.

3. Other changed environmental factor(s) are of greater importance to the vegetation.

These latter two reasons are considered in more detail below.

Vegetation change as a result of a relatively modest climate change (as opposed to an immediately catastrophic change like fire) could be expected to be slow. This is particularly true in the uplands, which are characterised by soils with inherently low nutrient availability. Plant species in such environments often have an intrinsically slow growth rate as an adaptation to limited nutrient supply (Chapin, 1980). Some may also be long-lived, and thus there may be a considerable lag before the effects of the climate change are seen at the level of the individual plant and subsequently in the community. As well as direct effects, indirect effects might also be of importance. As discussed in Chapter 5 the climatic amelioration has presumably produced a small net annual increase in the rate of nutrient cycling (production and mineralisation). Such changes are most likely to have had a cumulative effect on the vegetation over several years, rather than an immediate effect.

Few examples exist in the literature of vegetation responses at the decadal level to modest climatic warming. Pollen analysis tends to focus on vegetation changes at millennial timescales and even fine-resolution studies usually concentrate on intervals of around a century (Turner & Peglar, 1988). Experiments to warm vegetation tend to be short-term in nature and generally induce dramatic step changes above ambient, for example by 3 °C (Hillier, Sutton & Grime, 1994) or 5 °C (Chapin & Shaver, 1985). It is perhaps not surprising that rapid responses are then observed in experimental plots. Based on this limited evidence for responses over short timescales to dramatic warming however, it might be expected that 25 years would be sufficient to observe changes in the vegetation of Widdybank Fell as a response to more modest climate amelioration.

In terms of accounting for the observed vegetation changes on Widdybank Fell therefore, other environmental factors appear to be of greater importance than the climate moderation produced by the reservoir. These factors were discussed in Chapter 6 and it was concluded that some of the observed changes in the vegetation can be best accounted for as a response to atmospheric deposition. Based on the limited evidence available, nitrogen deposition did not seem to be having a discernible effect on higher plants, but could be responsible for the observed loss of bryophyte diversity and lichen abundance. The cumulative effect of acid deposition is the most likely cause of the decline in calcareous soil preferring species on the limestone grasslands. These conclusions are speculative, based upon the type of vegetation change seen and the evidence for changes in factors such as atmospheric deposition. Considerable future work is required in this area and important questions to be addressed include:

1. What nutrient is the greatest limiting factor to growth on Widdybank Fell? There may clearly be different answers to this question depending on the plant communities and the different soil types. Some of the sugar limestone grasslands are apparently limited in available phosphorus (Jeffrey, 1973) but nitrogen may well be the limiting factor in other plant communities. Answering this question is important for assessing the future impacts of environmental change, particularly nitrogen deposition. Microcosm fertilisation experiments, as described in Chapter 7 would be one method of answering this question and could be used to establish realistic "critical loads" of nitrogen.

2. What changes have there been in the soils on Widdybank Fell as a result of acid and nitrogen deposition? (why are conditions becoming deleterious for "stress tolerators" and calcicoles in particular?). Detailed soil chemical analysis compared to the survey of Jones (1973) might help to reveal answers to this complex question.

### *8.3 Implications for future management and conservation*

It is perhaps encouraging that from the evidence presented in this thesis there appear to have been few changes in the frequency or abundance of the "Teesdale rarities" on the sugar limestone grasslands since the early 1970s. Additionally, the interface between the different vegetation types on the fell has remained intact (except for some slight changes in the grass/heath boundary on the limestone heath). The changes in the vegetation have largely involved species of less immediate conservation interest. These results to date may be important for future environmental impact assessments for proposed reservoirs. From this study it has been shown that even a small water body can produce a significant "lake effect" but surrounding areas of vegetation are unlikely to be adversely affected. The greatest impact of the construction of Cow Green Reservoir seen so far has been the loss of the vegetation that was submerged.

The stated aim of English Nature for reserves such as Upper Teesdale is to protect and maintain the current levels of species diversity (Chris McCarty, site manager *pers. comm.*). Most of the factors potentially responsible for the observed vegetation changes (such as atmospheric deposition) are outside the control of reserve managers. There is one significant exception, however.

As described in Chapter 6, English Nature has recently taken the decision to reduce the number of sheep grazing on the fell. Given the results from this survey, particularly that the rarities are largely unchanged in abundance, reducing the grazing pressure would appear to be unnecessary. It is hard to predict the effect of this decision on the species and communities of highest conservation interest, so a monitoring programme will be vital and should be made a funding priority. Many of the "Teesdale rarities" have different reproductive strategies so it is probably impossible to find an optimum level of grazing for them all. For example, *Polygala amarella* has low seed production and no capability for vegetative reproduction, whereas *Gentiana verna* has the potential for successful reproduction both by seed and vegetative means (Bradshaw, 1978). Relatively low levels of grazing could favour the former species, but would not be essential for the latter (although the potential for genetic recombination to occur more frequently would be advantageous). Low grazing pressure could be deleterious for other species though, particularly *Draba incana.* Although this species reproduces by seed and thus might be thought to benefit from reduced grazing pressure, it is dependent on open habitats for successful regeneration (Doody, 1975) and would be intolerant of a tall, closed sward.

The decision to reduce grazing pressure on Widdybank Fell may have to be reviewed if the vegetation is becoming coarse or species-poor. Alternatively, it may be most beneficial to apply different levels of grazing pressure over a cycle of several years, for example a year in which the fell was left ungrazed could be followed by heavy grazing in the subsequent year to return to a short sward. The next three to four years could consist of modest grazing to maintain the low sward height and keep the more vigorous species in check. In order to closely monitor the effects of reduced grazing regime. point quadrat studies similar to that of Maxwell (1997) would be of particular use to detect subtle changes in vegetation composition.

### 8.4 Global warming: predictions and consequences

One significant threat to the future of semi-natural vegetation in Britain is global warming. This section considers some of the potential effects of a warming climate and provides the context for assessing Cow Green Reservoir as a potential model for climate change.

A number of models have been developed to predict future climate scenarios. For example, HADCM2 SUL predicts that by the period 2035-2064 mean summer and winter temperatures in Britain will have increased by 1.2-1.6 °C compared to the period 1961-1990 (Raper *et al.*, 1997). To put this change in context it should be noted that the Holocene (the c. 10000 year period since the last glacial) is considered to have been relatively stable climatically (Hulme & Barrow, 1997a). It has been estimated that mean temperatures have not changed by more than 1 °C in the British Isles during this time (Hulme & Barrow, 1997a). Hence the predicted rise in mean temperatures will be the greatest in the Holocene.

What is the likely response of British plant species to such a change? It has been demonstrated that taxa respond individualistically to climate change, for example Huntley and Birks (1983) and primarily by migration (Huntley & Webb, 1989) rather than evolutionary adaptation (Huntley, Bartlein & Prentice, 1989). Plant communities can therefore be seen as temporary associations of species rather than units responding cohesively to climate change (Graham & Grimm, 1990; Huntley, 1991; Huntley, *et al.*, 1997). Some species will be more immediately sensitive to the climate change than others. This will depend primarily on their range of tolerance to summer and winter mean and extreme temperatures (Saetersdal & Birks, 1997). Some species will clearly find the change favourable. In areas such as Upper Teesdale "lowland species" are likely to be most favoured. If such species prove aggressive competitors, they could potentially threaten the continued survival of the Teesdale rarities, resulting in a habitat of reduced conservation interest.

Moore *et al.* (1996) suggest that most plant species could survive the climate changes predicted for the next century, provided two conditions are met:

1. Species should have high inherent genetic variability so that at least some ecotypes will find the climate change favourable. (Unfortunately many British species of highest conservation interest are those that occur only in small, isolated populations with a narrow base of genetic diversity).

2. There should be no geographical boundaries such as mountain ranges preventing the migration of the species to more suitable environments if necessary i.e. there should be "wildlife corridors" along which species can migrate to new areas. (Unfortunately, in addition to natural geographic boundaries, semi-natural habitats in Britain and Europe are often isolated fragments surrounded by areas of intensive agriculture or urban development, which provide equally difficult barriers to cross).

Even if suitable and accessible habitats at higher elevation or latitude exist there is evidence that plant migration may not be able to keep pace with such rapid climatic warming as is predicted. Using historical records Grabherr, Gottfried and Pauli (1994) found a general trend for upward migration of the nival flora of the central Alps. Rates of movement for nine typical nival species over the last 70-90 years ranged from <1-4 m per decade. This movement was less than the 8-10 m per decade calculated as necessary to keep pace with the warming that had occurred over this period. If many of these species are to survive it is likely that human intervention will be required to move them to the more suitable sites that they cannot reach unaided.

### *8.5 Cow Green Reservoir as a model for climate change*

The demonstrated modification of the local climate produced by Cow Green reservoir provides an interesting model of climate change. In some respects, this climate change is similar to the predicted effects of global warming in Britain in the next fifty years. For example, mean summer temperature will have increased to around 1.2-1.6 °C by 2035-2064 according to HADCM2 SUL (Raper *et al.*, 1997). Mean summer temperature at Widdybank had increased due to the presence of the reservoir by only c. 0.25 °C (in the anomaly with respect to 1968) compared to Moor House, but the more noticeable changes were in the summer/autumn moderation of grass minimum temperatures by up to 2 °C (c. 1 °C on average). In addition, it is predicted that in Britain winters will be milder with fewer days of frost or snow lying (Barrow & Hulme, 1996; Raper *et al.*, 1997), again similar to the effects produced by the reservoir.

Some predicted effects of global warming are not equivalent to any produced by the reservoir. These include increased seasonality in rainfall, with winters in Northern England becoming wetter and summers dryer (observed by Burt *et al.*, 1998, see Chapter 6). Clearly also the rapid filling of the reservoir produced a virtual "step change" in local climate over a period of a few months, whereas global warming will occur more gradually.

Altogether, the predicted effects of global warming and those produced by the reservoir do share many similarities. Given these similarities, what can the responses of the vegetation at Widdybank tell us about the future for other areas of semi-natural vegetation and for species in climatically marginal habitats? It was fortunate that many of the species on Widdybank Fell were those which should have been particularly sensitive to warming (as described at the start of this chapter). This made their lack of apparent response after 25 years to the presence of the reservoir particularly interesting.

In the quest to predict the implications of global warming it is clearly important to remember that other environmental influences do not remain static. The effect of deposition of atmospheric pollutants appears to be of primary importance in explaining the changes in species composition in the vegetation on Widdybank Fell. Additionally, moderate changes in grazing pressure have the potential for affecting species composition on the fell quite dramatically. It is important to avoid what Hulme and Barrow (1997b) describe as climate change determinism. This is the tendency to assume that climate is the major controlling factor in all systems and to disregard other important factors such as changes in land use. Equally, it must be remembered that there is considerable potential for complex, synergistic effects between these changing environmental factors. For example, a warmer climate, increased nitrogen supply and increased concentrations of atmospheric $CO_2$ could increase the growth rates of some plant species considerably. In the long-term, this could affect the relative competitive success between species and thus the composition of the vegetation.

It is also clear that in the short-term at least, species may be surprisingly robust in their lack of response to climate change. This certainly appears to be the case for the vegetation of Widdybank Fell. Using modelling studies of species distributions Saetersdal and Birks (1997) found that mountain species in Norway had a surprisingly broad range of tolerance to mean January and July temperatures. The authors suggest that over the next few decades, most of these species may be relatively insensitive to the direct effects of climate change.

Finally, we must be prepared for the consequences when critical climatic thresholds for survival by plant species *are* exceeded. Huntley (1991) suggests that nature reserves could progressively lose the very species they were established to protect, so a more flexible approach to conservation will be required. He suggests that this could involve protected areas being linked by "wildlife corridors" to aid migration. Alternatively, seed from threatened species could be "artificially dispersed" to more favourable areas that they could not reach unaided.

The continued importance of monitoring the vegetation at Widdybank cannot be overstated. The plant species on the fell have already received considerable amelioration of their climate. In future, the additional effect of global warming may mean that these species are among the first to respond. They may provide a useful warning that critical thresholds are about to be reached for other upland plant species.

Indeed, the international significance of Widdybank Fell is now no longer just because of its unique flora and vegetation, but because of the wealth of research that has been carried out at this site. The collection of data on climate, atmospheric deposition, soils, plant communities and individual species already spans decades, and further monitoring will prove invaluable for understanding the processes of habitat responses to environmental change. The existence on the fell of vegetation types common to many upland areas means that the response of economically important species to environmental change can also be determined.

### *8.6 Conclusion*

The impact of Cow Green Reservoir on the local climate of Widdybank Fell has been demonstrated. However there is little evidence that the changes observed in the vegetation can be attributed to this climate change, and acid and nitrogen deposition are more likely to be responsible. The local climate change produced by Cow Green Reservoir in some respects acts as a model for predicted global warming. The lack of response to the climate change by potentially sensitive species on Widdybank Fell is perhaps encouraging. It implies that in the short-term at least, other species in semi-natural upland habitats may be relatively insensitive to warming. The importance of continued monitoring of the vegetation of Widdybank Fell has also been emphasised. The long-term future for many plant species on the fell is uncertain, but it is clear that active management will continue to be important in maintaining this internationally important site. Future questions that need to be addressed include:

1. Over what distance does the reservoir exert its climatic-moderating effect and how does the effect diminish with distance (linear or exponential)? A network of dataloggers on the fell could be used to provide the answer. It would be interesting also to investigate differences in rates of soil mineralisation with distance from the reservoir. If there was a discernible increase in mineralisation close to the reservoir edge this would provide an interesting analogue for the changes that might be observed in a future, warming climate.

2. In the long-term what species may potentially colonise Widdybank Fell as a result of the ameliorated climate or other environmental changes? The main change observed between the two vegetation surveys has been loss of species or decline in species abundance. There is clearly the potential for "new" species to take advantage of the changed environment.

3. What are the most important future synergisms between environmental change factors? Perhaps the combination of increased carbon dioxide concentrations and increased supply of nitrogen from the atmosphere will be most important

for plant growth. Additionally, rates of soil mineralisation and nutrient turnover could be dramatically enhanced in a warmer climate. It is important that a holistic approach to environmental change is adopted rather than considering the impact of changing environmental factors in isolation.

### *8.7 Summary*

- The changes observed in the vegetation of Widdybank Fell are discussed. It is concluded that whilst Cow Green reservoir has produced a discernible physical effect on the local climate, there are few changes in the vegetation that can be directly attributed to its effect. The effects of atmospheric deposition are most likely to be responsible for the observed vegetation changes.

- There have been few apparent changes in frequency or abundance of the "Teesdale rarities" between the two vegetation surveys. This is encouraging, but continued monitoring of the rarities and the vegetation in general is recommended. This is particularly needed in the short-term to assess the impact of reduced grazing pressure on the fell.

- The future fate of many of the rare species under predicted global warming scenarios is of concern, especially as there is nowhere of higher altitude or latitude that they could migrate to without human aid. This is true for many other species in semi-natural habitats.

- The local climate change produced by Cow Green reservoir is considered as a potential analogue for predicted climate change in Britain. The similarities between the effect of the reservoir and the predicted warming over the next fifty years are considerable. Based upon the findings of this thesis and other evidence, it is concluded that upland species may be relatively insensitive to the predicted climate change in Britain, at least in the short-term. The consequences when climatic limits are exceeded could, however, be severe.

## Thesis summary


- Upper Teesdale in the Northern Pennines is internationally renowned for its assemblage of phytogeographically disjunct species including arctic-alpines (e.g. *Gentiana verna*) and species of more southerly distribution (e.g. *Helianthemum canum*). The "Teesdale rarities" are particularly associated with the unique outcrops of metamorphosed "sugar" limestone. In 1965 it was proposed that a dam should be constructed on the river Tees to create a water-storage reservoir. This proposal was opposed by ecologists because of the loss (through submersion) of the plant communities on the western slopes of Widdybank Fell. In addition there was potential for the reservoir to produce an amelioration of the local climate that could prove deleterious to the remaining rare species, particularly those for which Teesdale was their most southerly locality. Parliament overruled these objections and the completed reservoir first began to fill in 1971.

- An extensive vegetation survey of Widdybank Fell was carried out prior to reservoir construction by Jones (1973). 31 plant communities were identified and mapped. The main purpose of this thesis was to repeat elements of the vegetation survey and determine the causal factors of any change. Nine plant communities originally defined by Jones were resurveyed, including the communities on the sugar limestone soils. The original quadrats used by Jones had not been marked in the field, but with the aid of sketch and vegetation maps their approximate positions could be relocated. Comparison between the two surveys showed significant changes in the composition of five out of the nine communities examined, with a general loss in bryophyte diversity and lichen abundance. Most of the individual species that had changed significantly had also declined in abundance, for example *Thymus praecox* subsp. *arcticus* had decreased in seven of the communities. There had been little change in the "Teesdale rarities" however. A systematic analysis was carried out of the ecological and physiological traits shared by the species

which had changed in abundance between the two surveys. This showed that species that had declined tended to be classified as "stress tolerators" and on the limestone grasslands it was the calcareous soil-preferring species that had declined.

- It was decided to investigate a number of environmental factors that could have changed in the period between the two vegetation surveys, changes in : the local climate (produced by Cow Green Reservoir), the regional climate, in atmospheric concentrations of carbon dioxide, in atmospheric deposition, or changes in grazing pressure on Widdybank Fell.

- In order to detect changes in the local climate produced by Cow Green Reservoir, meteorological records from Widdybank were compared with records from the nearby Moor House. It was found that the reservoir had produced a classic "lake effect", with cooler spring and warmer autumn temperatures and an all year round moderation of minima. Interestingly though, a comparison of the composition of selected plant communities close to and further from the influence of the reservoir revealed no difference with distance. There had been some changes in the regional climate since reservoir construction, but these were of smaller magnitude than the effects produced by the reservoir. It was concluded that from the available evidence, grazing pressure on Widdybank Fell had not changed considerably between the two vegetation surveys. Whilst atmospheric levels of carbon dioxide are rising, it was hard to attribute any of the observed changes to this cause. Levels of atmospheric nitrogen deposition have increased on the fell and are probably responsible for the loss of bryophyte diversity. Acid deposition has declined, but the cumulative effects could still be of significance, particularly for the calcicole species that are declining on the limestone grasslands.

- A microcosm experiment was established to investigate the temperature sensitivity of selected species collected from Widdybank Fell and placed along an altitudinal gradient. The species that were selected had changed in abundance since the survey of Jones (1973) and thus might be considered to be the most climatically sensitive. The altitudinal gradient comprised a lowland site (Durham) two upland sites of similar altitude (Widdybank Fell and Moor House) and a high upland site (Great Dun Fell). It was found that the species used *were* temperature sensitive when placed at the sites at the extreme end of the transect, but there was no difference in species performance between Widdybank and Moor House (the major difference between these two sites was an impounded versus an unimpounded catchment). Hence the species used were relatively insensitive to minor climatic differences.

- It was concluded that despite the evidence for local climate change produced by Cow Green Reservoir, the changes observed in the vegetation of Widdybank Fell since reservoir construction could not readily be attributed to its influence. Instead, the impacts of atmospheric deposition are probably more important. The effect of Cow Green upon the local climate bears some similarity to the predicted effects of global warming in Britain, and thus implies that many upland species may be relatively insensitive to future warming, at least in the short-term. The case for future monitoring of the responses of the vegetation of Widdybank Fell to environmental change is considerable, given the extensive baseline data already collected.

## References

**Adamson, J. K., Rowland, A. P., Scott, W. A. & Hornung, M.** (1996) Changes in soil acidity and related variables over 25 years in the North Pennine Uplands, UK. *Soil Use and Management* **12**: 55-61.

**Ågren, C.** (1993) $SO_2$ emissions: the historical trend. Acid News: A newsletter from the Swedish and Norwegian NGO Secretariats on acid rain. **5:** 1-4.

**Backhouse, J.** (1844) *The Phytologist* **1**.

**Bakker, J. P. & Berendse, F.** (1999) Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology and Evolution* **14**(2): 63-68.

**Balme, O. E.** (1954) Biological flora of the British Isles: *Viola lutea* Huds. *Journal of Ecology* **42**(1): 234-240.

**Barrow, E. & Hulme, M.** (1997) Describing the surface climate of the British Isles. In: *Climates of the British Isles: present, past and future*. M. Hulme & E. Barrow. Routledge, London.

**Barrow, E. M. & Hulme, M.** (1996) The changing probabilities of daily temperature extremes in the UK related to future global warming and changes in climate variability. *Climate Research* **6**: 21-31.

**Bellamy, D. J.** (1965) Conservation and Upper Teesdale. In: *The Natural History of Upper Teesdale*. D. H. Valentine. Tyne Printing Works Ltd., Newcastle upon Tyne.

**Bellamy, D. J., Bridgewater, P., Marshall, C. & Tickle, W. M.** (1969) Status of the Teesdale Rarities. *Nature* **222**.

**Bennett, M. D.** (1971) The duration of meiosis. *Proceedings of the Royal Society of London* **178 B**: 277-299.

**Beyers, R. J. & Odum, H. T.** (1993) *Ecological Microcosms.* Springer-Verlag, New York.

**Birse, E.L.** (1982) Plant communities on serpentine in Scotland. *Vegetatio* **49**: 141-162.

**Blackburn, K. B.** (1931) The Late-glacial and Post-glacial periods in the North Pennines. II. Possible survivals in our flora. *Transactions of the Northern Naturalist's Union* **1**: 32-.

**Bobbink, R. & Willems, J. H.** (1987) Increasing dominance of *Brachypodium pinnatum* (L.) Beauv in chalk grasslands: A threat to a species-rich ecosystem. *Biological Conservation* **40**: 301-314.

**Boulton, G. S.** (1977) A British ice sheet model. In: *British Quaternary Studies-Recent Advances.* F. W. Shotton.

**Bradshaw, M. E.** (1965) Upper Teesdale in danger. *Countryside* **20**(5).

**Bradshaw, M. E.** (1966) Upper Teesdale and the proposed reservoir. British Association for the Advancement of Science, Nottingham.

**Bradshaw, M. E.** (1978) Plant population studies and their relevance to nature conservation. *Biological Conservation* **14**: 223-242.

**Bradshaw, M. E.** (1981) Monitoring grassland plants in Upper Teesdale, England. In: *The Biological Aspects of Rare Plant Conservation.* H. Synge. John Wiley and Sons Ltd.

**Bradshaw, M. E. & Jones, A. V.** (1976) Phytosociology in Upper Teesdale: Guide to the vegetation maps of Widdybank Fell. University of Durham.

**Burdon, J. J.** (1983) Biological Flora of the British Isles: *Trifolium repens* L. *Journal of Ecology* **71**: 307-330.

**Burt, T. P., Adamson, J. K. & Lane, A. M. J.** (1998) Long-term rainfall and streamflow records for north central England: putting the Environmental Change Network site at Moor House, Upper Teesdale, in context. *Hydrological Sciences* **43**(5): 775-787.

**Chapin, F. S.** (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* **11**: 233-260.

**Chapin, F. S. & Shaver, G. R.** (1985) Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology* **66**(2): 564-576.

**Clapham, A. R.** (1978) Introduction. In: *Upper Teesdale- The area and its natural history.* Collins, London: 238.

**Clapham, A. R., Tutin, T. G. & Moore, D. M.** (1987) *Flora of the British Isles.* Cambridge University Press, Cambridge.

**Coulson, J. C.** (1978) Terrestrial animals. In: *Upper Teesdale: The area and its natural history.* A. R. Clapham. Collins, London.

**Crowe, P. R.** (1971) *Concepts in climatology.* Longman Group Limited, London.

**Dahl, E.** (1951) On the relation between summer temperature and the distribution of alpine vascular plants in the lowlands of Fennoscandia. *Oikos* **3**: 22-52.

**Devore, J. & Peck, R.** (1993) *Statistics: The exploration and analysis of data.* Wadsworth, Belmont, California.

**Dixon, J. M.** (1996) Waterlogging and survival in *Sesleria albicans. New Phytologist* **133**: 415-422.

**Doody, J. P.** (1975) *Studies in the population dynamics of some Teesdale plants.* PhD Thesis, University of Durham.

**During, H. J. & Willems, J. H.** (1986) The impoverishment of the bryophyte and lichen flora of the Dutch chalk grasslands in the thirty years 1953-1983. *Biological Conservation* **36**: 143-158.

**Ekstam, U., Jacobson, R., Mattson, M., Porsne, T.** (1984) *Ölands och Gotlands växtvärld.* Natur och Kultur, Stockholm.

**Elkington, T. T.** (1978) Phytogeography, Variation and Evolution. In: *Upper Teesdale: the area and its natural history.* A. R. Clapham. William Collins Sons & Co Ltd, Glasgow.

**Elkington, T. T.** (1981) Effects of excluding grazing animals from grassland on sugar limestone in Teesdale, England. *Biological Conservation* **20**: 25-35.

**Ellenberg, H.** (1988) *Vegetation ecology of central Europe.* Cambridge University Press, Cambridge.

**Elsworth, S.** (1984) *Acid rain.* Pluto Press Limited, London.

**Evans, G. C.** (1972) *The quantitative analysis of plant growth.* Blackwell Scientific Publications, Oxford.

**Fearn, G. M.** (1971) *Biosystematic studies of selected species in the Teesdale flora.* PhD Thesis, University of Sheffield.

**Fraser, L. H. & Keddy, P.** (1997) The role of experimental microcosms in ecological research. *Trends in Ecology and Evolution* **12**(12): 478-481.

**Garnett, M. H., Ineson, P. & Adamson, J. K.** (1997) A long-term upland temperature record: no evidence for recent warming. *Weather* **52**: 342-351.

**Gilbert, O. L.** (1970) Further studies on the effects of sulphur dioxide on lichens and bryophytes. *New Phytologist* **69**: 605-627.

**Gimingham, C. H.** (1960) Biological flora of the British Isles: *Calluna vulgaris* (L.) Hull. *Journal of Ecology* **48**: 455-483.

**Gimingham, C. H.** (1975) *An introduction to heathland ecology.* Oliver and Boyd.

**Godwin, H.** (1949) The spreading of the British flora considered in relation to conditions of the late-glacial period. *Journal of Ecology* **37**: 140-147.

**Godwin, H. & Walters, S. M.** (1967) The scientific importance of Upper Teesdale. *Proceedings of the Botanical Society of the British Isles* **6**(4): 348-351.

**Gore, A. J. P.** (1968) The supply of six elements by rain to an upland peat area. *Journal of Ecology* **56**: 483-495.

**Grabherr, G., Gottfried, M. & Pauli, H.** (1994) Climate effects on mountain plants. *Nature* **369**: 448.

**Graham, R. W. & Grimm, E. C.** (1990) Effects of global climate change on the patterns of terrestrial biological communities. *Trends in Ecology and Evolution* **5**(9): 289-292.

**Gregory, R.** (1975) The Cow Green Reservoir. In: *The politics of political resources*. P. J. Smith. Penguin, Harmondsworth.

**Gregory, S. & Smith, K.** (1967) Local temperature and humidity contrasts around small lakes and reservoirs. *Weather* **22**: 497-505.

**Grime, J. P.** (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* **111**(982): 1169-1194.

**Grime, J. P., Hodgson, J. G. & Hunt, R.** (1988) *Comparative Plant Ecology- A functional approach to common British species*. Unwin Hyman Ltd, London.

**Grime, J. P. & Mowforth, M. A.** (1982) Variation in genome size- an ecological interpretation. *Nature* **299**: 151-153.

**United Kingdom Climate Change Impacts Review Group** (1996) Review of the potential effects of climate change in the United Kingdom (2nd Report). Department of the Environment.

**Harding, R. J.** (1979) A note on the effect of the Cow Green Reservoir on the local climate. *Journal of the Institute of water engineers and scientists* **33**: 252-254.

**Harrison, A. F., Taylor, K., Hatton, J. C. & Howard, D. M.** (1994) Role of nitrogen in herbage production by *Agrostis-Festuca* hill grassland. *Journal of Applied Ecology* **31**: 351-360.

**Hebeisen, T., Lüscher, A., Zanetti, S., Fischer, B. U., Hartwig, U. A., Frehner, M., Hendrey, G. R., Blum, H. & Nösberger, J.** (1997) Growth response of *Trifolium repens* L. and *Lolium perenne* L. as monocultures and bi-species mixture to free air $CO_2$ enrichment and management. *Global Change Biology* **3**: 149-160.

**Heil, G. W. & Diemont, W. H.** (1983) Raised nutrient levels change heathland into grassland. *Vegetatio* **53**: 113-120.

**Hill, M. O. & Preston, C. D.** (1998) The geographical relationships of British and Irish bryophytes. *Journal of Bryology* **20**: 127-226.

**Hillier, S. H., Sutton, F. & Grime, J. P.** (1994) A new technique for the experimental manipulation of temperature in plant communities. *Functional Ecology* **8**: 755-762.

**Hornung, M.** (1968) *The morphology, mineralogy and genesis of some soils on the Moor House National Nature Reserve*. PhD Thesis, University of Durham.

**Hornung, M.** (1994) Impacts of nitrogen deposition in terrestrial ecosystems. United Kingdom Review Group on Impacts of Nitrogen Deposition on Terrestrial Ecosystems.

**Houghton, J. T., Filho, L. G. M., Callander, B. A., Harris, N., Kattenberg, A. & Maskell, K.**, Eds. (1996) *Climate Change 1995: The science of climate change*. Cambridge University Press, Cambridge.

**Hulme, M. & Barrow, E.** (1997a) *Climates of the British Isles, present, past and future*. Routledge, London.

**Hulme, M. & Barrow, E.** (1997b) Introducing climate change. In: *Climates of the British Isles: present, past and future.* M. Hulme & E. Barrow. Routledge, London.

**Hunt, R., Hand, D. W., Hannah, M. A. & Neal, A. M.** (1991) Response to $CO_2$ enrichment in 27 herbaceous species. *Functional Ecology* **5**: 410-421.

**Hunt, R., Hand, D. W., Hannah, M. A. & Neal, A. M.** (1993) Further responses to $CO_2$ enrichment in British herbaceous species. *Functional Ecology* **7**: 661-668.

**Huntley, B.** (1991) How plants respond to climate change: Migration rates, individualism and the consequences for plant communities. *Annals of Botany (Supplement)* **67**: 15-22.

**Huntley, B., Bartlein, P. J. & Prentice, I. C.** (1989) Climatic control of the distribution and abundance of beech (*Fagus* L.) in Europe and North America. *Journal of Biogeography* **16**: 551-560.

**Huntley, B., Baxter, R., Lewthwaite, K. J., Willis, S. G. & Adamson, J. K.** (1998) Vegetation responses to local climatic changes induced by a water-storage reservoir. *Global Ecology and Biogeography letters* **7**: 241-257.

**Huntley, B. & Birks, H. J. B.** (1983) *An atlas of past and present pollen maps for Europe: 0-13000 years ago.* Cambridge University Press, Cambridge.

**Huntley, B., Cramer, W., Morgan, A. V., Prentice, H. C. & Allen, J. R. M.** (1997) *Past and future rapid environmental changes: the spatial and evolutionary responses of terrestrial biota.* Springer, Berlin.

**Huntley, B. & Webb, T.** (1989) Migration: species' response to climatic variations caused by changes in the earth's orbit. *Journal of Biogeography* **16**: 5-9.

**Ivimey-Cook, R. B. & Proctor, M. C. F.** (1966) The plant communities of the Burren, Co. Clare. *Proceedings of the Royal Irish Academy* **64 (Section B)**(15): 211-301.

**Jeffrey, D. W.** (1971) The experimental alteration of a *Kobresia* rich sward in Upper Teesdale. In: *The scientific management of animal and plant communities for conservation (Symposium of the BES no. 11)*. E. Duffey & A. S. Watt. Blackwell, Oxford.

**Jeffrey, D. W.** (1987) *Soil-plant relationships: an ecological approach.* Croom Helm, London.

**Jeffrey, D. W. & Piggott, C. D.** (1973) The response of grasslands on sugar-limestone in Teesdale to application of phosphorus and nitrogen. *Journal of Ecology* **61**: 85-92.

**Johnson, G. A. L., Robinson, D. & Hornung, M.** (1971) Unique bedrock and soils associated with the Teesdale flora. *Nature* **232**: 453-456.

**Jones, A. V.** (1973) *A phytosociological study of Widdybank Fell in Upper Teesdale*. PhD Thesis, University of Durham.

**Jones, P. D. & Conway, D.** (1997) Precipitation in the British Isles: An analysis of area-average data updated to 1995. *International Journal of Climatology* **17**: 427-438.

**Kennedy, A. D.** (1995) Simulated climate change: are passive greenhouses a valid microcosm for testing the biological effects of environmental perturbations? *Global Change Biology* **1**: 29-42.

**Kershaw, K. A. & Looney, J. H. H.** (1985) *Quantitative and dynamic plant ecology.* Edward Arnold, London.

**Körner, C.** (1995) Impact of atmospheric changes on alpine vegetation: the ecophysiological perspective. In: *Potential ecological impacts of climate change in the Alps and Fennoscandian mountains.* A. Guisan *et al.*,. Conserv. Jard. Bot., Geneva.

**Körner, C. & Menendez-Riedl, S. P.** (1989) The significance of developmental aspects in plant growth analysis. In: *Causes and consequences of variation in growth rate and productivity of higher plants.* H. Lambers. SPB Academic Publishers, The Hague.

**Kuylenstierna, J. C. I. & Chadwick, M. J.** (1991) Increases in soil acidity in north-west Wales between 1957 and 1990. *Ambio* **20**: 118-119.

**Lee, J. A., Tallis, J. H. & Woodin, S. J.** (1998) Acidic deposition and British upland vegetation. In: *Ecological change in the uplands: Special publication No. 7 of The British Ecological Society.* Eds. M. B. Usher & D. B. A. Thompson. Blackwell, Oxford.

**Lousley, J. E.** (1965) The threat to Upper Teesdale. The Botanical Society of the British Isles.

**Malloch, A. J. C.** (1992) MATCH: A computer program to aid the assignment of vegetation data to the communities and subcommunities of the National Vegetation Classification. University of Lancaster.

**Manley, G.** (1968) *Climate and the British scene*. Collins, London.

**Maxwell, F.** (1997) *Microclimatic effects upon the composition of grassland species on Widdybank Fell, Upper Teesdale NNR.* MSc Thesis, University of Durham.

**Meteorological Office.** (1982) *Observer's Handbook.* Her Majesty's Stationary Office, London.

**Meusel, H. & Jager, E. J.** (1992) *Vergleichende Chorologie der Zentraleuropaischen flora.* Gustav Fischier Verlag Jena, Stuttgart.

**Mooney, H. A., Drake, B. G., Luxmoore, R. J., Oechel, W. C. & Pitelka, L. F.** (1991) Predicting ecosytem responses to elevated $CO_2$ concentrations. *BioScience* **41**(2): 96-104.

**Moore, P. D., Chaloner, B. & Stott, P.** (1996) *Global environmental change.* Blackwell Science Ltd, Oxford.

**Morecroft, M. D., Sellers, E. K. & Lee, J. A.** (1994) An experimental investigation into the effects of atmospheric nitrogen deposition on two semi-natural grasslands. *Journal of Ecology* **82**: 475-483.

**Naeem, S., Thompson, L. J., Lawler, S. P., Lawton, J. H. & Woodfin, R. M.** (1994) Declining biodiversity can alter the performance of ecosystems. *Nature* **368**: 734-737.

**Newton, P. C. D.** (1991) Direct effects of increasing carbon dioxide on pasture plants and communities. *New Zealand Journal of Agricultural Research* **34**: 1-24.

**Nugent** (1978) Preface. In: *Upper Teesdale: The area and its natural history*. A. R. Clapham. Collins, Glasgow.

**Pastor, J., Stillwell, M. A. & Tilman, D.** (1987) Nitrogen mineralisation and nitrification in four Minnesota old fields. *Oecologia* **71**: 481-485.

**Pearson, J. & Stewart, G. R.** (1993) Tansley Review No. 56: The deposition of atmospheric ammonia and its effects on plants. *New Phytologist* **125**: 283-305.

**Pigott, C. D.** (1956) The vegetation of Upper Teesdale in the North Pennines. *Journal of Ecology* **44**(2): 545-586.

**Pigott, C. D.** (1978a) Climate and Vegetation. In: *Upper Teesdale: The Area and its Natural History*. A. R. Clapham. Collins, Glasgow.

**Pigott, C. D.** (1978b) Geology, Soils and Vegetation. In: *Upper Teesdale: The Area and its Natural History*. A. R. Clapham. Collins, Glasgow.

**Pigott, C. D. & Walters, S. M.** (1954) On the interpretation of the discontinuous distributions shown by certain British species of open habitats. *Journal of Ecology* **42**: 95-116.

**Pitcairn, C. E. R., Fowler, D. & Grace, J.** (1991) Changes in species composition of semi-natural vegetation associated with the increase in atmospheric inputs of N. Nature Conservancy Council.

**Poore, M. E. D.** (1955) The use of phytosociological methods in ecological investigations Part II. *Journal of Ecology* **43**: 245-269.

**Preston, C. D. & Hill, M. O.** (1997) The geographic relationships of British and Irish vascular plants. *Botanical Journal of the Linnean Society* **124**: 1-120.

**Purvis, O. W., Coppins, B. J., Hawksworth, D. L., James, P. W. & Moore, D. M.** (1992) *The lichen flora of Great Britain and Ireland.* Natural History Museum Publications, London.

**Raper, S., Viner, D., Hulme, M. & Barrow, E.** (1997) Global warming and the British Isles. In: *Climates of the British Isles: present, past and future.* M. Hulme & E. Barrow. Routledge, London.

**Ratcliffe, D. A.** (ed.) (1977) *A nature conservation review.* Vol. 2: Site accounts. Cambridge University Press, Cambridge.

**Ratcliffe, D. A.** (1978) Plant Communities. In: *Upper Teesdale- The area and its natural history.* A. R. Clapham. William Collins Sons & Co Ltd, Glasgow.

**RGAR** (1990) Acid deposition in the United Kingdom 1986-1998. Third report of the United Kingdom Review Group on Acid Rain. Stevenage, Warren Spring Laboratory.

**Roberts, B. K.** (1978) Man and Land in Upper Teesdale. In: *Upper Teesdale: The Area and its Natural History.* A. R. Clapham. William Collins Sons & Co Ltd, Glasgow.

**Rodwell, J. S.** (1992a) *British Plant Communities, Volume 2: Mire and heaths.* Cambridge University Press.

**Rodwell, J. S.** (1992b) *British Plant Communities, Volume 3: Grasslands and montane communities.* Cambridge University Press.

**Saetersdal, M. & Birks, H. J. B.** (1997) A comparative ecological study of Norwegian mountain plants in relation to possible future climatic changes. *Journal of Biogeography* **24**: 127-152.

**Sage, R. F., Sharkey, T. D. & Seeman, J. R.** (1989) Acclimation of photosynthesis to elevated $CO_2$ in five $C_3$ species. *Plant Physiology* **89**: 590-596.

**Salisbury, F. B. & Ross, C. W.** (1992) *Plant Physiology.* Wadsworth, California.

**Scott, C. M. (1997)** *An investigation into the distribution and abundance of* Achillea millefolium *L. in grassland on Widdybank Fell, Upper Teesdale NNR.* MSc Thesis, University of Durham.

**Shimwell, D. W.** (1971) *The description and classification of vegetation.* Billing & Sons Limited, London.

**Smith & Sowerby** (1798) *English Botany.*

**Smith, A. J. E.** (1980) *The Moss Flora of Britain and Ireland.* Cambridge University Press, Cambridge.

**Smith, A. J. E.** (1990) *The liverworts of Britain and Ireland.* Cambridge University Press, Cambridge.

**Sokal, R. R. & Rohlf, F. J.** (1969) *Biometry : The principles and practice of statistics in biological research.* Freeman, San Francisco.

**TerBraak, C. J. F.** (1988) CANOCO- an extension of DECORANA to analyse species-environment relationships. *Vegetatio* **75**: 159-160.

**Trist, P.J.O.** (ed.) (1979). *An ecological flora of Breckland.* E P Publishing Limited, Wakefield.

**Turner, J.** (1978) The History of the Vegetation and Flora. In: *Upper Teesdale: The Area and its Natural History*. A. R. Clapham. Collins, Glasgow.

**Turner, J., Hewetson, V. P., Hibbert, F. A., Lowry, K. H. & Chambers, C.** (1973) The history of the vegetation and flora of Widdybank Fell and the Cow Green reservoir basin, Upper Teesdale. *Philosophical Transactions of the Royal Society of London, B* **265**(327-408).

**Turner, J. & Peglar, S. M.** (1988) Temporally-precise studies of vegetation history. In: *Vegetation History*. B. Huntley & T. Webb. Kluwer Academic Publishers, Dordrecht.

**Valentine, D. H.** (1976) *The Natural History of Upper Teesdale*. Tyne Printing Works Ltd, Newcastle upon Tyne.

**Valentine, D. H. & Harvey, M. J.** (1961) *Viola rupestris* Schmidt in Britain. *Proceedings, The Botanical Society of the British Isles* **4**: 129-135.

**Vincent, K. J., Campbell, G. W., Downing, C. E. H., Hasler, S. E., Davies, M., Stedman, J. R., Sansom, L. E., Briscombe, C. & Page, H. M.** (1996) Acid deposition monitoring in the United Kingdom: the first ten years. AEA Technology plc. Oxford.

**Walter, H.** (1979) *Vegetation of the Earth*. Springer-Verlag, New York.

**Warwick, S. I. & Black, L.** (1982) The Biology of Canadian Weeds. 52. *Achillea millefolium* L. *Canadian Journal of Plant Science* **62**: 163-182.

**Watson, E. V.** (1968) *British mosses and liverworts*. Cambridge University Press, Cambridge.

**Watt, A. S.** (1960) Population changes in acidophilous grass-heath in Breckland 1936-1957. *Journal of Ecology* **48**: 605-629.

**Weiher, E. & Keddy, P. A.** (1995) The assembly of experimental wetland plant communities. *Oikos* **73**: 323-335.

**Welch, D. & Rawes, M.** (1972) Moisture regimes of soils on metamorphosed limestone in Upper Teesdale. *Transactions of the Natural History Society of Northumberland, Durham and Newcastle upon Tyne. New Series* **17**: 57-67.

**Whitehead, S. J., Caporn, S. J. M. & Press, M. C.** (1997) Effects of elevated $CO_2$, nitrogen and phosphorus on the growth and photosynthesis of two upland perennials: *Calluna vulgaris* and *Pteridium aquilinum. New Phytologist* **135**: 201-211.

**Wigley, I. M. L., Jones, P. D. & Briffa, K. R.** (1987) Cross-dating methods in dendrochronlogy. *Journal of archeological science* **14**: 51-64.

**Willis, S. G.** (1995) *An investigation into changes in composition and distribution of the vegetation of Widdybank Fell, Upper Teesdale during the last twenty years.* MSc Thesis, University of Durham.

**Wilson, E. J., Wells, T. C. E. & Sparks, T. H.** (1995) Are calcareous grasslands in the UK under threat from nitrogen deposition? - an experimental determination of a critical load. *Journal of Ecology* **83**: 823-832.

**Wolfenden, J. & Diggle, P. J.** (1995) Canopy gas exchange and growth of upland pasture swards in elevated $CO_2$. *New Phytologist* **130**: 369-380.

**Woodin, S. J.** (1988) Acidic deposition and upland conservation: an overview and the way ahead. In: *Ecological change in the uplands: Special publication No.*

*7 of the British Ecological Society*. M. B. Usher & D. B. A. Thompson. Blackwell, Oxford.

**Woodward, F. I., Thompson, G. B. & McKee, I. F.** (1991) The effects of elevated concentrations of carbon dioxide on individual plants, populations, communities and ecosystems. *Annals of Botany* **67**: 23-38.

**Wulff, R. D. & Alexander, H. M.** (1985) Intraspecific variation in the response to $CO_2$ enrichment in seeds and seedlings of *Plantago lanceolata* L. *Oecologia* **66**: 458-460.

# Appendices

**Table (i) Field key to plant communities on Widdybank Fell in the Class Festuco-Brometea, Association Seslerio-Caricetum pulicaris. Based on Jones (1973). Species in brackets occurred with low constancy in the association as a whole, but were still designated as differentials.**

**Differential species for the Association Seslerio-Caricetum pulicaris**
*Sesleria albicans, Koeleria macrantha, Danthonia decumbens, Gentianella amarella, Helianthemum nummularium, Plantago maritima, Cladonia subrangiformis, C. pocillum, Cetraria islandica, Coelocaulon aculeatum, Tortella tortuosa, Racomitrium canescens, Ditrichum flexicaule, (Viola rupestris, Antennaria dioica, Avenula pratensis)*

- *Minuartia verna*
  - *Carex ericetorum*
    - **Differential species for Nodum 1**
      *Kobresia simpliciuscula*
    - **Differential species for Nodum 2**
      *Rhytidium rugosum*
  - **Differential species for Nodum 3**
    *Carex capillaris, C. caryophyllea, Gentiana verna, Cladonia arbuscula*
- *Carex pulicaris, Polygonum viviparum, Carex capillaris, C. caryophyllea, Gentiana verna, Cladonia arbuscula*
  - *Rhytidiadelphus squarrosus, Pleurozium schreberi, Hypnum jutlandicum*
    - **Differential species for Nodum 4**
      *Calluna vulgaris, Polygala serpyllifolia, Agrostis stolonifera, Rhytidiadelphus loreus*
    - **Differential species for Nodum 5**
      *Plantago lanceolata, Hieracium pilosella, Thuidium tamariscinum*
  - *Kobresia simpliciuscula*
    - **Differential species for Nodum 6**
      None
      i.e. absence of Nodum 7 differential species is diagnostic
    - **Differential species for Nodum 7**
      *Primula farinosa, Carex hostiana, C. lepidocarpa*

**Table (ii) Field key to plant communities on Widdybank Fell in the Class Molinio-Arrhenatheretea, Association Festuco-Nardetum. Based on Jones (1973). The only nodum in this association examined in the present study was Nodum 21.**

- **Differential species for the Association Molinio-Arrhenatheretea**
  *Trifolium repens, Plantago lanceolata, Ranunculus acris*
  - *Carex pulicaris, C. flacca, C. panicea, Bellis perennis, Agrostis stolonifera, Deschampsia cespitosa*
    - *Carex demissa, C. capillaris, Festuca rubra, Plantago maritima, Taraxacum officinale, Ctendium molluscum, Bryum pseudotriquetrum, Ditrichum flexicaule, Leontodon autumnalis*
      - **Differential species for Nodum 19**
        *Cardamine pratensis, Climacium dendroides, Drepanocladus revolvens*
      - **Differential species for Nodum 20**
        *Sesleria albicans, Nardus stricta, Linum catharticum, Campylium stellatum*
    - **Differential species for Nodum 21**
      *Sesleria albicans, Koeleria macrantha, Nardus stricta, Danthonia decumbens, Carex caryophyllea, C. pilulifera, Viola lutea, Achillea millefolium, Alchemilla glabra*
  - **Differential species for Nodum 22**
    *Galium saxatile, Anthoxanthum odoratum, Agrostis vinealis*

**Table (iii) Field key to plant communities on Widdybank Fell in the Class Nardo-Callunetea "Association" *Vaccinium myrtillus* heath complex. Based on Jones (1973). Species in bold type were those used in the identifcation of a stand of vegetation as Nodum 33, the only nodum in this association examined in the present study.**

- **Differential species for the *Vaccinium myrtillus* heath complex**
  *Hypnum ericetorum, Galium saxatile, Calluna vulgaris, Dicranum scoparium, Pleurozium schreberi, Cladonia arbuscula, Vaccinium myrtillus, Nardus stricta*
  - **Differential species for Nodum 26**
    *Empetrum nigrum, Erica tetralix, Trichophorum cespitosum, Molinia caerulea, Campylopus paradoxus, Carex binervis*
  - *Carex pilulifera, Polytrichum formosum, Polygala serpyllifolia*
    - **Differential species for Nodum 31**
      *Deschampsia flexuosa, Pteridium aquilinum, Parmelia physodes, Pohlia nutans, Blechnum spicant*
    - *Campanula rotundifolia, Agrostis stolonifera, Luzula campestris, Briza media, Cladonia subrangifomis, Ptilidium ciliare*
      - **Differential species for Nodum 32**
        *Viola riviniana, Viola lutea, Anthoxanthum odoratum, Cetraria islandica, Thymus praecox sp. arcticus, Racomitrium lanuginosum, Hylocomium splendens, Koeleria macrantha, Dicranum bonjeanii*
      - **Differential species for Nodum 33**
        *Danthonia decumbens, Carex caryophyllea*

# Appendix B

**The Domin Scale** - as used by Jones (1973) and in the present survey. This scale was somewhat unconventional compared to the scale used by Kershaw and Looney (1985) and appeared to be based mainly on Shimwell (1971).

| | |
|---|---|
| 1 | scarce, 1-2 individuals, cover small |
| 2 | less than 1 % |
| 3 | 1 to 4 % |
| 4 | abundant, cover 5 to 20 % |
| 5 | abundant, cover 20 to 25 % |
| 6 | 25 to 33 % |
| 7 | 33 to 50 % |
| 8 | 50 to 75 % |
| 9 | 75 to 90 % |
| 10 | 90 to 100 % |

In order for the data from the present and original surveys to be comparable, species entries recorded on the Domin scale as + by Jones i.e. "single individual "was changed to 1 i.e. "cover small" for the purposes of numerical analysis. (The + notation was not used in data collection in the present survey). Bare ground was scored as a percentage by Jones; this was converted into the relevant point on the Domin scale in order to be compared with the data collected in the present survey.

**Origin of relevés**

Some of the relevés recorded by Jones (1973) in Noda 1-7 were surveyed from Cronkley Fell rather than Widdybank Fell. Such noda were not separately identified and were used in the subsequent phytosociological classification. It was however possible to determine which relevés definitely originated from Widdybank, either because they appeared on a sketch map of Widdybank (see columns 2 and 3 of Table (i)) or because the relevé contained species not found on Cronkley Fell (starred relevés in column 4 of Table (i)). Only these relevés which definitely originated from Widdybank were used in subsequent analysis. Quadrat 358 (Nodum 33) was positioned on the vegetation map of Sand Sike (Sheet 2) based on an aerial photograph. This quadrat was most accurately placed slightly outside the coloured area of the vegetation map, but was used for analysis. Quadrats 115 and 315 (Nodum 5) were most accurately placed in an area marked as Nodum 6 by Jones on the vegetation map Sheet 3. This designation as Nodum 6 is likely to be an error as the sketch maps are unequivocal in their positioning and the vegetation on the ground today is clearly Nodum 5.

**Table (i) List of all quadrat numbers recorded by the survey of Jones (1973) for the nine noda under study, divided according to whether or not their postions could be used in the present survey. Also included is the list of the additional quadrats surveyed.**

| Nodum | Quadrat positions appearing on sketch maps which could be used in the present survey | Quadrat positions appearing on sketch maps which could not be used in the present survey | Quadrat positions not on any surviving map | Additional quadrats used in the present survey |
|---|---|---|---|---|
| 1 | 308 309 310 348 516 | | 300* 301* | 800-805 |
| 2 | 307 341 343 344 347 518 | | (374) 302* 303* (369) (371) (428) | 806-809 |
| 3 | 107 118 335 | 104 323 | 4 8 9 73 (368) (373) | 810-816 |
| 4 | 80 97 102 103 105 110 116 316 317 319 325 339 | | | |
| 5 | 98 113 115 120 122 134 137(h/h) 138 306 312 313 315 322 329 | 95 135 330 340 | 3 5 6 71* 72 75 76 109 125 299 353 364 365 366 (367) | 817-818 |
| 6 | 96 99 108 311 324 327 328 332 333 334 336 337 508 | | 74 124 331 338 | |
| 7 | 13 63 65 81 94 106 112 117 119 | 111 136 | 77 78* | 819 |
| 21 | 121(h/h) 127 137(h/h) 504 (h/h) | 236 355 | 126 397 | 820-826 |
| 33 | 357 358 360 | 494 | 129 130 438 | 827-833 |

**Key**

h/h after a species number indicates a hummock-hollow complex composed of two noda. One or both of the noda represented may have been surveyed depending on the method of Jones.

( ) indicates a quadrat surveyed by Jones on Cronkley Fell (identified by the presence of certain species in the quadrat not found on Widdybank e.g. *Dryas octopetala*).

* indicates a quadrat surveyed by Jones on Widdybank Fell (identified by the presence of certain species not found on Cronkley Fell e.g. *Viola rupestris*).

**Table (ii) Complete species list from both the original and present surveys for the nine selected noda, with frequency values (F) and median score on the Domin scale (D). Species appearing in bold type are those for which there was a significant difference in frequency or abundance between surveys in at least one nodum in the Mann-Whitney test (*c.f.* Table 3.3).**

| | NODUM 1 | | | | NODUM 2 | | | | NODUM 3 | | | | NODUM 4 | | | | NODUM 5 | | | | NODUM 6 | | | | NODUM 7 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | |
| Number of species recorded | 43 | | 54 | | 45 | | 52 | | 56 | | 68 | | 95 | | 63 | | 111 | | 87 | | 73 | | 57 | | 96 | | 66 | |
| | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D |
| *Achillea millefolium* | | | | | | | | | | | | | | | | | 0.42 | 2 | 0.44 | 2 | | | | | 0.17 | 1 | 0.10 | 2 |
| ***Agrostis capillaris*** | | | **0.09** | **3** | | | | | | | **0.10** | **3** | **0.42** | **1** | **0.83** | **3** | **0.05** | **2** | **0.81** | **3** | | | **0.08** | **3** | **0.33** | **1** | **0.30** | **3** |
| ***Agrostis stolonifera*** | | | | | | | | | | | **0.10** | **2** | **0.50** | **2.5** | | | | | | | **0.08** | **2** | | | **0.17** | **1.5** | **0.10** | **2** |
| ***Agrostis vinealis*** | | | | | | | | | | | | | | | **0.50** | **3** | | | | | | | | | | | | |
| *Alchemilla filicaulis* subsp. *vestita* | | | | | | | | | | | | | | | | | | | 0.13 | 1.5 | | | | | | | | |
| *Alchemilla glabra* | | | | | | | | | | | | | 0.08 | 1 | | | 0.11 | 1.5 | 0.19 | 2 | 0.08 | 1 | | | | | | |
| *Andreaea rothii* | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.10 | 2 |
| ***Anemone nemorosa*** | | | | | | | | | | | | | | | **0.50** | **2** | **0.05** | **2** | **0.06** | **1** | | | | | | | | |
| *Aneura pinguis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Antennaria dioica* | 0.14 | 2 | 0.09 | 3 | | | | | 0.40 | 2 | 0.20 | 2.5 | 0.17 | 2.5 | 0.08 | 1 | 0.37 | 2 | 0.19 | 3 | 0.15 | 1.5 | 0.31 | 2 | 0.17 | 1.5 | | |
| ***Anthoxanthum odoratum*** | | | | | | | | | | | | | **0.17** | **1.5** | **0.75** | **2** | **0.05** | **1** | **0.06** | **3** | | | | | | | | |
| *Anthyllis vulneraria* | | | | | 0.13 | 1 | 0.20 | 2 | | | | | | | | | | | | | 0.05 | 1.5 | 0.08 | 3 | | | | |
| *Armeria maritima* | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.10 | 1 |
| *Atrichum undulatum* | | | | | | | | | | | | | | | | | 0.05 | 2 | | | | | | | | | | |
| *Avenula pratensis* | 0.29 | 3 | 0.09 | 2 | 0.25 | 1.5 | 0.10 | 2 | | | | | 0.17 | 1 | | | 0.16 | 2 | 0.13 | 2 | 0.08 | 2 | | | 0.42 | 2 | | |
| *Bacidia lignaria* | | | | | | | | | | | | | | | | | 0.05 | 4 | | | 0.08 | 1 | | | 0.08 | 1 | | |
| *Baeomyces rufus* | | | | | | | | | 0.20 | 2 | 0.10 | 1 | 0.17 | 1 | | | | | | | | | | | | | | |
| *Barbilophozia barbata* | | | | | | | | | | | | | | | | | 0.11 | 1.5 | | | 0.08 | 1 | | | 0.08 | 2 | | |
| *Barbilophozia floerkei* | | | | | | | | | | | | | 0.08 | 2 | | | 0.16 | 1 | | | | | | | | | | |
| *Barbula cylindrica* | | | 0.09 | 2 | | | | | | | | | | | | | | | | | | | | | | | | |

## Table (ii) continued

| | NODUM 1 | | | | NODUM 2 | | | | NODUM 3 | | | | NODUM 4 | | | | NODUM 5 | | | | NODUM 6 | | | | NODUM 7 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | |
| | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D |
| *Barbula reflexa* | | | | | 0.13 | 1 | | | 0.20 | 1 | | | | | | | | | | | | | | | | | | |
| *Barbula unguiculata* | | | | | | | | | | | | | 0.08 | 1 | | | | | | | | | | | | | | |
| *Bellis perennis* | | | | | | | 0.10 | 1 | | | | | | | | | 0.05 | 4 | 0.25 | 1.5 | | | 0.08 | 2 | 0.17 | 1 | | |
| *Botrychium lunaria* | | | | | | | | | | | | | 0.08 | 1 | 0.08 | 1 | | | 0.13 | 1.5 | | | | | | | | |
| *Brachythecium velutinum* | | | | | | | | | | | | | | | | | | | | | | | | | 0.08 | 1 | | |
| ***Briza media*** | **0.71** | **3** | **0.45** | **3** | **0.63** | **2** | **0.50** | **3** | **0.80** | **4** | **0.90** | **3** | **1.00** | **3** | **0.42** | **3** | **0.95** | **4** | **0.75** | **3.5** | **0.92** | **4** | **0.92** | **3** | **1.00** | **3** | **1.00** | **3** |
| *Bryum caespiticium* | | | | | | | | | | | | | 0.08 | 2 | | | | | | | | | | | | | 0.10 | 2 |
| *Bryum capillare* | | | | | | | | | | | 0.1 | 2 | | | | | | | | | | | | | 0.08 | 1 | | |
| *Bryum pallens* | | | | | | | | | | | | | | | | | 0.05 | 1 | 0.06 | 1 | | | | | 0.08 | 1 | | |
| *Bryum pseudotriquetrum* | | | | | 0.25 | 2 | | | | | | | 0.08 | 3 | | | 0.05 | 1 | | | | | | | 0.17 | 1.5 | | |
| *Calliergon cuspidatum* | | | | | 0.25 | 2 | | | | | | | | | | | 0.16 | 2 | | | | | | | 0.42 | 1 | 0.10 | 1 |
| ***Calluna vulgaris*** | | | **0.09** | **4** | | | | | **0.20** | **1** | **0.20** | **3** | **0.83** | **8** | **1.00** | **9** | | | **0.19** | **4** | **0.08** | **2** | | | **0.08** | **1** | **0.20** | **2.5** |
| ***Campanula rotundifolia*** | **0.71** | **2** | **0.55** | **2** | **0.25** | **1.5** | **0.40** | **2** | **0.80** | **3** | **0.90** | **2** | **0.92** | **3** | **1.00** | **2** | **1.00** | **3** | **0.88** | **2** | | | **0.85** | **2** | **0.75** | **3** | **0.70** | **2** |
| *Campylium chrysophyllum* | | | | | | | | | 0.20 | 2 | | | | | | | 0.11 | 2.5 | | | 0.08 | 1 | | | 0.17 | 1 | | |
| *Campylium stellatum* | | | | | | | | | | | | | | | | | | | | | | | | | 0.17 | 1.5 | | |
| *Campylopus fragilis* | | | 0.27 | 2 | | | 0.20 | 1.5 | | | 0.3 | 2 | 0.08 | 1 | | | | | | | 0.08 | 1 | 0.15 | 1 | 0.08 | 1 | 0.20 | 2 |
| *Cardamine pratensis* | | | | | | | | | | | | | 0.08 | 1 | | | | | | | | | | | | | | |
| *Carex binervis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| ***Carex capillaris*** | | | **0.09** | **3** | | | **0.10** | **2** | **0.80** | **4.5** | **0.5** | **2** | **0.08** | **1** | **0.08** | **2** | **0.79** | **4** | **0.75** | **2.5** | **0.77** | **3** | **0.15** | **2** | **0.92** | **2** | **0.50** | **2** |
| ***Carex caryophyllea*** | | | | | | | **0.10** | **3** | **0.80** | **2** | **0.2** | **2.5** | **0.92** | **3** | **1.00** | **2** | **0.84** | **2.5** | **0.88** | **2.5** | **0.31** | **2** | | | **0.33** | **1.5** | **0.30** | **3** |
| *Carex demissa* | | | | | | | | | | | | | 0.08 | 1 | | | 0.05 | 2 | | | | | | | | | | |
| *Carex ericetorum* | 0.71 | 4 | 0.18 | 3 | 0.50 | 3 | 0.50 | 2 | | | | | 0.08 | 2 | | | 0.05 | 3 | 0.19 | 2 | | | | | | | 0.30 | 3 |
| *Carex flacca* | 0.43 | 3 | 0.55 | 3 | 0.25 | 2.5 | 0.60 | 2.5 | 0.60 | 1 | 0.5 | 3 | 0.83 | 2 | 0.75 | 2 | 0.89 | 2 | 0.69 | 4 | 0.77 | 2 | 0.77 | 3 | 0.92 | 3 | 0.80 | 4 |
| ***Carex hostiana*** | | | | | | | | | | | | | **0.17** | **2** | | | | | | | | | | | **0.58** | **3** | | |
| *Carex lepidocarpa* | | | | | | | | | | | | | | | | | 0.05 | 1 | | | | | | | 0.42 | 1 | 0.30 | 3 |

**Table (ii) continued**

| | NODUM 1 | | | | NODUM 2 | | | | NODUM 3 | | | | NODUM 4 | | | | NODUM 5 | | | | NODUM 6 | | | | NODUM 7 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | |
| | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D |
| ***Carex panicea*** | 0.29 | 1 | 0.82 | 3 | | | 0.20 | 3 | 0.80 | 3 | 0.7 | 3 | 1.00 | 3 | 0.50 | 2.5 | 0.68 | 3 | 0.50 | 3 | 0.85 | 3 | 0.85 | 3 | 0.92 | 3 | 0.80 | 3.5 |
| ***Carex pilulifera*** | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| ***Carex pulicaris*** | | | | | | | | | | | | | 0.92 | 3 | 0.33 | 2 | 0.68 | 3 | 0.31 | 3 | 0.38 | 1 | | | 0.42 | 3 | | |
| *Cephalozia bicuspidata* | | | | | | | | | | | | | | | | | | | | | | | | | 0.08 | 1 | | |
| *Cerastium fontanum* | | | | | | | | | | | | | 0.08 | 2 | 0.08 | 1 | 0.26 | 1 | 0.25 | 1.5 | | | | | | | | |
| *Cetraria islandica* | 0.29 | 1 | 0.09 | 1 | 0.63 | 1 | 0.20 | 1 | 0.80 | 1 | 0.2 | 1 | 0.33 | 1 | 0.08 | 1 | 0.53 | 1 | 0.19 | 2 | 0.62 | 2 | 0.23 | 1 | 0.50 | 1 | | |
| *Cirsium palustre* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Cladonia ciliata* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| ***Cladonia arbuscula*** | 0.14 | 1 | | | | | | | 0.60 | 1 | 0.2 | 1 | 0.58 | 2 | 0.08 | 1 | 0.68 | 3 | 0.06 | 1 | 0.62 | 2 | | | 0.25 | 2 | | |
| *Cladonia cariosa* | | | | | | | | | | | | | | | | | | | | | | | | | 0.08 | 1 | | |
| *Cladonia chlorophaea* | | | | | | | | | | | | | 0.08 | 1 | 0.08 | 3 | | | | | 0.08 | 2 | | | | | | |
| *Cladonia coniocraea* | | | | | | | | | | | 0.1 | 1 | 0.17 | 1 | 0.08 | 1 | | | | | | | | | | | | |
| *Cladonia crispata* | | | | | | | | | | | | | | | | | | | 0.06 | 1 | | | | | | | | |
| *Cladonia furcata* | | | 0.09 | 1 | | | 0.20 | 1 | 0.20 | 1 | 0.7 | 1 | 0.08 | 2 | 0.08 | 1 | | | 0.25 | 1 | | | 0.31 | 1 | | | 0.10 | 1 |
| *Cladonia gracilis* | | | | | | | | | | | | | 0.08 | 1 | | | | | | | | | | | | | | |
| *Cladonia ochrochlora* | | | | | | | | | | | | | | | | | 0.05 | 2 | | | 0.08 | 1 | | | 0.08 | 1 | | |
| *Cladonia pityrea* | | | | | | | 0.20 | 1.5 | | | | | | | | | | | | | | | | | | | | |
| ***Cladonia pocillum*** | 0.57 | 1 | 0.09 | 1 | 0.50 | 1.5 | 0.20 | 1 | 0.60 | 1 | 0.4 | 1 | 0.50 | 2 | | | 0.26 | 2 | | | 0.54 | 2 | 0.08 | 1 | 0.42 | 2 | 0.10 | 1 |
| *Cladonia portentosa* | | | | | | | | | | | 0.1 | 2 | | | 0.33 | 1 | | | 0.19 | 2 | 0.08 | 2 | 0.08 | 1 | | | | |
| *Cladonia rangiformis* | | | 0.09 | 1 | | | 0.10 | 1 | 0.20 | 1 | 0.1 | 1 | | | 0.08 | 1 | 0.05 | 2 | 0.06 | 1 | 0.08 | 3 | 0.15 | 1.5 | 0.08 | 1 | 0.10 | 2 |
| ***Cladonia subrangiformis*** | 0.43 | 1 | 0.45 | 5 | 0.88 | 2 | | | 0.80 | 2 | | | 0.83 | 1 | | | 0.89 | 1 | | | 0.69 | 1 | | | 0.75 | 1 | | |
| *Cladonia subulata* | | | | | | | | | | | 0.1 | 1 | | | | | | | | | | | | | | | | |
| *Cladonia uncialis* | | | 0.09 | 1 | | | | | | | | | | | | | 0.05 | 2 | 0.13 | 1.5 | | | | | | | | |
| *Climacium dendroides* | | | | | | | | | | | | | | | | | 0.05 | 3 | | | | | | | | | | |
| ***Coelocaulon aculeatum*** | 0.43 | 1 | 0.09 | 1 | 1.00 | 1.5 | 0.30 | 1 | 0.80 | 1 | 0.50 | 1 | 0.17 | 1 | | | 0.63 | 1 | 0.25 | 2 | 0.38 | 2 | 0.08 | 1 | 0.33 | 1 | 0.10 | 2 |

## Table (ii) continued

| | NODUM 1 | | | | NODUM 2 | | | | NODUM 3 | | | | NODUM 4 | | | | NODUM 5 | | | | NODUM 6 | | | | NODUM 7 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | |
| | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D |
| *Cololejeunea calcarea* | | | | | | | | | | | | | | | | | | | | | | | | | 0.08 | 1 | | |
| ***Ctenidium molluscum*** | 0.86 | 2.5 | 0.55 | 2 | 0.63 | 2 | 0.80 | 1 | 0.80 | 1.5 | 0.60 | 1 | | | | | 0.42 | 2 | 0.19 | 1 | 0.85 | 2 | 0.62 | 1 | 1.00 | 4 | 0.60 | 2 |
| ***Danthonia decumbens*** | 0.57 | 1.5 | 0.18 | 3 | | | 0.10 | 2 | 0.40 | 1.5 | | | 0.42 | 1 | 0.17 | 1 | 0.68 | 3 | 0.06 | 3 | 0.62 | 2 | | | 0.67 | 2 | 0.40 | 3 |
| *Deschampsia cespitosa* | | | | | | | | | | | | | | | | | | | | | 0.08 | 4 | | | 0.17 | 1 | | |
| *Deschampsia flexuosa* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Dichodontium pellucidum* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Dicranum bonjeanii* | | | | | | | | | | | | | 0.50 | 2 | 0.08 | 1 | 0.32 | 2 | | | 0.23 | 2 | | | 0.08 | 3 | | |
| ***Dicranum scoparium*** | | | | | | | | | | | 0.10 | 1 | 0.33 | 3 | 0.50 | 2 | 0.21 | 1 | 0.69 | 1 | 0.15 | 2.5 | 0.31 | 2 | | | 0.10 | 2 |
| *Diplophyllum albicans* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| ***Ditrichum flexicaule*** | 0.71 | 2 | | | 1.00 | 2.5 | 0.50 | 2 | 1.00 | 2 | 0.70 | 2 | 0.08 | 2 | | | 0.47 | 2 | 0.25 | 1.5 | 0.62 | 2.5 | 0.23 | 2 | 1.00 | 2 | 0.30 | 2 |
| *Draba incana* | | | | | | | | | | | 0.20 | 1.5 | | | | | | | | | | | | | | | | |
| *Drepanocladus revolvens* | | | | | | | | | | | | | | | | | | | | | | | | | 0.25 | 1 | | |
| *Empetrum nigrum* | | | | | | | | | | | 0.10 | 4 | 0.08 | 1 | 0.08 | 2 | 0.11 | 5 | 0.06 | 4 | 0.08 | 6 | 0.08 | 4 | 0.08 | 3 | | |
| *Encalypta streptocarpa* | 0.14 | 2 | | | 0.13 | 1 | 0.20 | 1 | | | | | | | | | | | 0.06 | 1 | | | | | | | | |
| *Equisetum palustre* | | | | | | | | | | | | | | | | | | | | | | | 0.08 | 2 | | | | |
| *Equisetum variegatum* | | | | | | | | | | | | | | | | | | | | | 0.08 | 1 | | | | | | |
| ***Euphrasia rostkoviana*** | 0.86 | 2 | 0.09 | 2 | 0.63 | 1 | 0.60 | 1 | 1.00 | 3 | 1.00 | 1.5 | 0.67 | 2 | 0.33 | 1.5 | 1.00 | 3 | 0.69 | 1 | 1.00 | 4 | 0.54 | 2 | 0.92 | 3 | 0.80 | 1.5 |
| *Eurhynchium praelongum* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| ***Festuca ovina*** | 1.00 | 4 | 1.00 | 5 | 1.00 | 4 | 1.00 | 6 | 1.00 | 6 | 1.00 | 6 | 1.00 | 5 | 1.00 | 5 | 1.00 | 5 | 1.00 | 6 | 1.00 | 4 | 1.00 | 5 | 1.00 | 5 | 0.90 | 6 |
| *Festuca rubra* | | | | | | | | | | | | | | | | | | | | | | | | | 0.08 | 1 | | |
| ***Fissidens adianthoides*** | 0.43 | 1 | 0.27 | 2 | 0.25 | 2 | 0.20 | 1 | 0.40 | 2.5 | 0.30 | 1 | 0.08 | 1 | 0.08 | 1 | 0.53 | 2 | 0.19 | 2 | 0.54 | 1 | 0.23 | 1 | 0.92 | 2 | 0.40 | 1 |
| *Fissidens cristatus* | | | | | | | | | | | | | | | | | | | 0.06 | 1 | | | | | | | | |
| *Fissidens osmundoides* | | | | | | | | | | | | | | | | | 0.05 | 1 | | | | | | | | | | |
| ***Frullania tamarisci*** | 0.14 | 2 | | | 0.13 | 2 | | | 0.40 | 1.5 | | | 0.25 | 2 | | | 0.47 | 1 | 0.06 | 1 | 0.38 | 2 | | | 0.50 | 1.5 | | |
| *Galium boreale* | | | | | | | | | | | 0.10 | 2 | 0.17 | 1.5 | | | 0.05 | 1 | | | | | | | 0.25 | 3 | 0.40 | 2 |

## Table (ii) continued

| | NODUM 1 | | | | NODUM 2 | | | | NODUM 3 | | | | NODUM 4 | | | | NODUM 5 | | | | NODUM 6 | | | | NODUM 7 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | |
| | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D |
| *Galium saxatile* | | | | | | | | | | | | | 0.17 | 1.5 | 0.58 | 2 | 0.05 | 1 | | | | | | | | | | |
| ***Galium sterneri*** | **0.14** | **2** | **0.18** | **1** | **0.13** | **1** | **0.30** | **2** | **1.00** | **2** | **0.80** | **2** | **1.00** | **2** | **0.50** | **2** | **1.00** | **3** | **1.00** | **2** | **1.00** | **2** | **0.92** | **2** | **0.92** | **2** | **1.00** | **2** |
| *Galium verum* | | | | | | | | | | | | | 0.08 | 1 | | | 0.05 | 2 | 0.13 | 1 | | | | | 0.08 | 1 | 0.20 | 2.5 |
| *Gentiana verna* | | | 0.09 | 1 | | | | | 0.80 | 2 | 0.30 | 1 | 0.42 | 1 | 0.08 | 1 | 0.47 | 2 | 0.50 | 1 | 0.54 | 1 | 0.23 | 2 | 0.83 | 2 | 0.40 | 2 |
| ***Gentianella amarella*** | **0.14** | **1** | **0.55** | **1** | **0.25** | **1** | **0.60** | **1** | **0.40** | **1** | **0.90** | **2** | **0.08** | **1** | **0.08** | **1** | **0.58** | **1** | **0.63** | **2** | **0.62** | **1** | **0.69** | **2** | **0.58** | **1** | **0.70** | **2** |
| *Geum rivale* | | | | | | | | | | | | | | | | | 0.05 | 1 | 0.13 | 1 | | | | | | | | |
| *Helianthemum nummularium* | 0.71 | 3 | 0.55 | 3.5 | 0.88 | 4 | 0.80 | 4.5 | 0.60 | 4 | 0.80 | 3 | 0.17 | 3.5 | 0.08 | 1 | 0.47 | 4 | 0.44 | 4 | 0.69 | 3 | 0.69 | 3 | 0.33 | 3 | | |
| ***Hieracium pilosella*** | | | | | **0.13** | **1** | | | **0.20** | **2** | **0.40** | **2** | **0.08** | **1** | | | **0.53** | **1** | **0.75** | **3** | **0.08** | **4** | | | | | | |
| *Huperzia selago* | | | | | | | | | | | | | | | | | 0.05 | 1 | | | | | | | | | | |
| ***Hylocomium splendens*** | | | **0.09** | **2** | **0.13** | **1** | **0.20** | **1.5** | **0.60** | **1** | **0.20** | **2.5** | | | **0.75** | **2** | **0.79** | **2** | **0.56** | **2** | **0.15** | **1.5** | **0.08** | **2** | **0.50** | **2** | **0.50** | **1** |
| ***Hypnum cupressiforme* var. *lacunosum*** | **0.29** | **2** | **0.18** | **1.5** | **0.63** | **2** | **0.30** | **3** | **0.60** | **3** | **0.70** | **2** | **0.58** | **3** | **0.08** | **2** | **0.68** | **3** | **0.69** | **2** | **0.54** | **3** | **0.54** | **2** | **0.67** | **3** | **0.10** | **2** |
| *Hypnum cupressiforme* var. *resupinatum* | | | 0.18 | 1 | | | | | | | 0.10 | 1 | | | | | | | | | | | | | | | 0.10 | 1 |
| ***Hypnum jutlandicum*** | | | | | | | | | | | | | **0.58** | **4** | **0.83** | **3** | **0.53** | **4** | **0.25** | **2** | **0.15** | **2.5** | **0.08** | **1** | | | **0.20** | **1** |
| *Hypochoeris radicata* | | | | | | | | | | | | | | | | | | | | | | | | | 0.08 | 1 | | |
| *Juncus acutiflorus* | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.10 | 3 |
| *Juncus squarrosus* | | | | | | | | | | | | | | | | | 0.05 | 1 | | | | | | | | | | |
| *Kobresia simpliciuscula* | 0.86 | 3.5 | 0.82 | 4 | | | 0.30 | 2 | | | 0.30 | 4 | 0.08 | 2 | 0.08 | 2 | 0.05 | 2 | 0.19 | 3 | 1.00 | 4 | 0.92 | 4.5 | 1.00 | 7 | 0.90 | 4 |
| ***Koeleria macrantha*** | **0.86** | **2** | **0.27** | **3** | **0.88** | **3** | **0.40** | **2** | **1.00** | **3** | **0.60** | **3** | **0.83** | **2** | **0.42** | **3** | **1.00** | **3** | **0.88** | **3** | **0.92** | **2.5** | **0.23** | **2** | **1.00** | **2** | **0.50** | **3** |
| *Lathyrus montana* | | | | | | | | | 0.20 | 1 | | | 0.08 | 1 | 0.08 | 1 | | | | | | | | | | | | |
| *Leiocolea alpestris* | | | | | | | | | | | | | | | | | | | | | | | | | 0.08 | 1 | | |
| *Leontodon autumnalis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| ***Linum catharcticum*** | **0.71** | **1** | **0.73** | **1** | **0.63** | **2** | **0.40** | **1** | **1.00** | **3** | **1.00** | **2** | **0.33** | **2.5** | **0.50** | **1** | **0.89** | **3** | **0.63** | **1** | **0.92** | **2** | **1.00** | **1** | **0.92** | **3** | **1.00** | **2** |
| *Lophocolea bidentata* | | | | | | | | | | | | | 0.17 | 1.5 | | | 0.21 | 1 | | | | | | | 0.08 | 1 | | |

## Table (ii) continued

| | NODUM 1 | | | | NODUM 2 | | | | NODUM 3 | | | | NODUM 4 | | | | NODUM 5 | | | | NODUM 6 | | | | NODUM 7 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | |
| | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D |
| *Lophozia ventricosa* | | | | | | | | | | | | | | | | | | | | | 0.08 | 1 | | | | | | |
| *Lotus corniculatus* | | | | | 0.13 | 1 | | | | | 0.10 | 1 | 0.33 | 3 | 0.08 | 4 | 0.37 | 2 | 0.44 | 3 | 0.23 | 2 | 0.08 | 3 | 0.08 | 2 | | |
| *Luzula campestris* | | | | | | | | | | | | | 0.08 | 1 | | | 0.32 | 2 | 0.19 | 3 | | | | | | | | |
| *Minuartia verna* | 0.43 | 2 | 0.64 | 2 | 0.63 | 1 | 0.80 | 1.5 | 0.40 | 1 | 0.80 | 2 | | | | | 0.11 | 2 | 0.06 | 2 | 0.08 | 1 | 0.08 | 1 | 0.08 | 1 | | |
| *Mnium hornum* | | | | | | | | | | | | | 0.08 | 1 | | | | | | | | | | | | | | |
| *Molinia caerulea* | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.30 | 3 |
| *Nardus stricta* | | | | | | | | | | | | | 0.08 | 1 | | | | | | | | | | | | | | |
| *Peltigera canina* | | | 0.09 | 2 | | | 0.20 | 1 | | | 0.40 | 2 | | | | | 0.16 | 1 | 0.19 | 2 | 0.08 | 1 | 0.08 | 1 | | | | |
| *Peltigera leucophlebia* | | | | | | | | | 0.20 | 2 | | | 0.08 | 1 | | | 0.21 | 1 | | | 0.15 | 1 | | | | | | |
| *Peltigera praetextata* | | | | | | | | | | | | | | | | | 0.05 | 1 | | | | | | | 0.08 | 1 | | |
| *Philonotis fontana* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Pinguicula vulgaris* | | | | | | | | | | | | | | | | | 0.11 | 1 | | | | | | | 0.33 | 1 | 0.30 | 2 |
| *Placynthiella uliginosa* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| ***Plagiochila asplenioides*** | | | **0.09** | **2** | | | | | | | | | **0.33** | **1** | | | **0.53** | **1.5** | | | | | | | **0.42** | **1** | **0.10** | **1** |
| *Plagiomnium rostratum* | | | | | | | | | | | 0.10 | 1 | 0.17 | 1 | | | 0.16 | 1 | 0.06 | 1 | | | 0.08 | 1 | 0.08 | 1 | | |
| *Plagiomnium undulatum* | | | | | | | | | | | | | | | | | 0.11 | 1 | | | | | | | | | | |
| *Plantago lanceolata* | | | 0.09 | 2 | | | 0.10 | 2 | | | 0.30 | 2 | 0.17 | 1 | | | 0.53 | 2 | 0.44 | 3 | 0.08 | 1 | 0.15 | 2.5 | 0.25 | 1 | 0.30 | 2 |
| *Plantago major* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Plantago maritima* | 0.29 | 2 | 0.18 | 3 | 0.38 | 2 | 0.40 | 2.5 | 0.40 | 2 | 0.50 | 2 | 0.17 | 1.5 | | | 0.37 | 2 | 0.06 | 2 | 0.69 | 2 | 0.62 | 2 | 0.83 | 1 | 0.60 | 2 |
| ***Pleurozium schreberi*** | | | | | | | | | **0.20** | **1** | | | **0.92** | **2** | **0.67** | **2** | **0.37** | **1** | | | | | | | | | | |
| *Poa pratensis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Pohlia nutans* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Polygala amarella* | | | | | | | | | 0.20 | 2 | | | | | | | 0.11 | 1.5 | | | 0.46 | 1.5 | | | | | | |
| *Polygala serpyllifolia* | | | | | | | | | | | | | 0.50 | 2 | 0.83 | 1.5 | 0.21 | 4 | 0.13 | 1.5 | | | 0.08 | 2 | 0.08 | 1 | | |
| *Polygonum viviparum* | | | | | | | 0.10 | 1 | 0.20 | 1 | 0.10 | 2 | 0.25 | 1 | 0.08 | 1 | 0.53 | 3 | 0.44 | 2 | 0.38 | 2 | 0.46 | 2 | 0.58 | 3 | 0.30 | 2 |

**Table (ii) continued**

| | NODUM 1 | | | | NODUM 2 | | | | NODUM 3 | | | | NODUM 4 | | | | NODUM 5 | | | | NODUM 6 | | | | NODUM 7 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | |
| | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D |
| *Polytrichum commune* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Polytrichum formosum* | | | | | | | | | | | | | 0.25 | 2 | 0.17 | 1 | 0.37 | 3 | 0.13 | 2.5 | | | | | | | | |
| *Polytrichum juniperinum* | | | | | | | | | | | | | | | 0.08 | 2 | 0.05 | 2 | | | | | | | | | | |
| *Polytrichum piliferum* | | | | | | | | | | | | | | | | | 0.05 | 4 | | | | | | | | | | |
| *Potentilla crantzii* | | | | | | | | | 0.20 | 2 | | | 0.33 | 1.5 | | | 0.26 | 1 | | | 0.23 | 2 | | | | | | |
| ***Potentilla erecta*** | 0.14 | 1 | 0.18 | 2 | | | 0.10 | 4 | 0.80 | 2.5 | 0.50 | 2 | 0.92 | 4 | 1.00 | 3 | 0.95 | 3 | 0.94 | 2 | 0.77 | 2.5 | 0.77 | 2 | 1.00 | 4 | 1.00 | 2 |
| *Primula farinosa* | | | 0.09 | 2 | 0.13 | 1 | | | | | 0.10 | 1 | | | | | | | | | | | | | 0.83 | 2 | 0.50 | 2 |
| *Prunella vulgaris* | | | | | | | 0.10 | 3 | 0.20 | 2 | 0.30 | 2 | 0.08 | 4 | | | 0.47 | 2 | 0.50 | 2 | 0.15 | 2 | | | 0.67 | 1.5 | 0.80 | 2 |
| *Pseudoscleropodium purum* | | | 0.09 | 1 | | | 0.10 | 1 | 0.40 | 1 | 0.30 | 1 | 0.33 | 1 | 0.33 | 2 | 0.47 | 2 | 0.38 | 1.5 | 0.23 | 2 | 0.08 | 2 | 0.33 | 1 | 0.40 | 1.5 |
| *Ptilidium ciliare* | | | | | | | | | | | | | 0.17 | 1.5 | | | 0.11 | 4 | | | | | | | | | | |
| ***Racomitrium canescens*** | 0.43 | 2 | 0.09 | 2 | 0.75 | 2 | | | 0.80 | 3.5 | 0.20 | 2 | 0.08 | 2 | | | 0.42 | 2.5 | 0.25 | 2.5 | 0.46 | 2 | 0.15 | 1.5 | 0.50 | 1 | 0.30 | 1 |
| ***Racomitrium lanuginosum*** | 0.71 | 3 | 0.82 | 2 | 0.75 | 2.5 | 0.80 | 2 | 1.00 | 6 | 1.00 | 2 | 0.67 | 2.5 | 0.17 | 1.5 | 0.79 | 3 | 0.63 | 2 | 0.77 | 3 | 0.69 | 3 | 0.83 | 3 | 0.70 | 3 |
| *Ranunculus acris* | | | | | | | | | | | | | 0.33 | 1.5 | 0.08 | 2 | 0.05 | 2 | 0.06 | 1 | | | 0.08 | 1 | | | | |
| *Rhodobryum roseum* | | | | | | | | | | | | | | | | | | | 0.13 | 1 | | | | | | | | |
| ***Rhytidiadelphus loreus*** | | | | | 0.13 | 3 | | | | | | | 0.67 | 2 | | | 0.16 | 2 | | | | | | | | | | |
| *Rhytidiadelphus squarrosus* | 0.14 | 1 | 0.09 | 1 | | | 0.10 | 1 | | | 0.20 | 1.5 | 0.67 | 2 | 0.92 | 2 | 0.37 | 2 | 0.63 | 2 | 0.15 | 1.5 | 0.23 | 1 | 0.08 | 1 | | |
| *Rhytidiadelphus triquetrus* | | | | | | | 0.10 | 1 | | | 0.10 | 2 | 0.08 | 3 | | | 0.32 | 1.5 | 0.25 | 2 | | | | | 0.42 | 1 | 0.60 | 1 |
| *Rhytidium rugosum* | 0.14 | 7 | | | 0.63 | 5 | 0.60 | 1.5 | | | | | | | | | | | | | | | | | | | | |
| *Rumex acetosa* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Sanguisorba officinalis* | | | | | | | | | | | | | 0.33 | 1 | | | | | | | | | | | | | | |
| ***Scapania aspera*** | 0.71 | 2 | 0.09 | 1 | 0.50 | 2 | 0.10 | 1 | 0.80 | 2 | 0.20 | 1 | 0.17 | 2 | 0.08 | 1 | 0.74 | 1 | | | 0.85 | 2 | 0.08 | 1 | 1.00 | 2 | 0.10 | 1 |
| ***Selaginella selaginoides*** | 0.29 | 1.5 | 0.09 | 2 | 0.13 | 2 | | | 1.00 | 2 | 0.30 | 2 | 0.67 | 2 | 0.25 | 1 | 0.95 | 3 | 0.50 | 2 | 0.92 | 2 | 0.54 | 2 | 1.00 | 3 | 0.90 | 2 |
| ***Sesleria albicans*** | 1.00 | 6 | 0.91 | 5 | 1.00 | 4 | 0.80 | 6 | 1.00 | 4 | 1.00 | 4.5 | 1.00 | 4.5 | 0.83 | 4 | 0.95 | 6 | 0.88 | 4 | 1.00 | 5 | 1.00 | 6 | 1.00 | 6 | 1.00 | 5 |
| *Solorina saccata* | | | 0.09 | 1 | 0.13 | 3 | | | | | 0.10 | 3 | | | | | | | 0.13 | 1.5 | | | | | | | | |
| *Succisa pratensis* | | | | | | | | | | | 0.10 | 1 | 0.17 | 1 | 0.17 | 1.5 | 0.16 | 1 | 0.19 | 1 | 0.15 | 1 | 0.15 | 2.5 | 0.17 | 1 | 0.20 | 2.5 |

**Table (ii) continued**

| | NODUM 1 | | | | NODUM 2 | | | | NODUM 3 | | | | NODUM 4 | | | | NODUM 5 | | | | NODUM 6 | | | | NODUM 7 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | | Original | | Present | |
| | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D | F | D |
| *Taraxacum officinale* | | | | | 0.13 | 1 | | | | | 0.10 | 2 | | | 0.08 | 1 | 0.11 | 2 | 0.13 | 1.5 | | | | | 0.08 | 1 | | |
| *Thalictrum alpinum* | | | | | | | | | | | | | 0.25 | 2 | 0.08 | 1 | | | 0.06 | 2 | | | 0.15 | 1.5 | 0.25 | 2 | 0.20 | 1.5 |
| *Thuidium delicatulum* | | | | | | | | | | | | | | | | | | | | | | | | | 0.08 | 1 | | |
| *Thuidium philibertii* | | | | | 0.13 | 1 | | | | | | | | | | | 0.11 | 2.5 | | | | | | | 0.08 | 1 | | |
| *Thuidium tamariscinum* | | | | | | | | | | | | | 0.08 | 1 | | | 0.32 | 1 | 0.06 | 1 | 0.08 | 1 | | | 0.08 | 1 | | |
| ***Thymus praecox* subsp. *arcticus*** | **1.00** | **5** | **1.00** | **3** | **1.00** | **4** | **0.90** | **3** | **1.00** | **4** | **1.00** | **3** | **0.92** | **4** | **0.92** | **4** | **1.00** | **5** | **0.94** | **3** | **1.00** | **4** | **1.00** | **3** | **1.00** | **4** | **1.00** | **3** |
| *Tofieldia pusilla* | | | | | | | | | | | | | | | | | | | | | | | | | 0.17 | 2.5 | 0.20 | 2 |
| ***Tortella tortuosa*** | **1.00** | **4** | **0.73** | **2** | **1.00** | **4** | **1.00** | **2.5** | **1.00** | **3** | **0.80** | **2** | **0.17** | **2** | **0.08** | **1** | **0.47** | **2** | **0.31** | **2** | **0.69** | **3** | **0.62** | **1.5** | **0.92** | **3** | **0.80** | **2** |
| *Trichostomum brachydontium* | 0.14 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Trifolium repens* | | | | | | | 0.10 | 1 | 0.20 | 1 | | | | | 0.08 | 3 | 0.37 | 2 | 0.50 | 2 | | | | | | | 0.10 | 2 |
| *Tritomaria quinquedentata* | | | | | | | | | | | | | | | | | 0.05 | 2 | | | | | | | | | | |
| *Trollius europaeus* | | | | | | | | | | | | | 0.17 | 1 | | | | | | | | | | | 0.17 | 1 | | |
| *Vaccinium myrtillus* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Veronica officinalis* | | | | | | | | | | | | | | | | | 0.11 | 1.5 | 0.06 | 1 | | | | | | | | |
| *Vicia orobus* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Vicia sativa* | | | | | | | | | | | | | | | | | | | 0.06 | 1 | | | | | | | | |
| ***Viola lutea*** | | | **0.09** | **1** | | | **0.10** | **2** | **0.20** | **1** | **0.10** | **2** | **0.17** | **1.5** | **0.33** | **2** | **0.37** | **2** | **0.81** | **2** | | | | | **0.08** | **1** | **0.30** | **2** |
| *Viola riviniana* | 0.14 | 1 | 0.36 | 1 | | | 0.30 | 2 | 1.00 | 1 | 0.90 | 1 | 1.00 | 3 | 1.00 | 3 | 0.95 | 2 | 1.00 | 2 | 0.77 | 1.8 | 0.54 | 1 | 0.75 | 2 | 0.60 | 2 |
| *Viola riviniana* x *rupestris* | 0.14 | 1 | | | | | | | | | | | | | | | 0.05 | 1 | | | | | | | | | | |
| ***Viola rupestris*** | **0.86** | **3.5** | **0.64** | **2** | **0.88** | **3** | **0.60** | **2.5** | **0.20** | **4** | **0.1** | **2** | | | | | **0.05** | **2** | **0.06** | **2** | **0.15** | **3** | **0.23** | **2** | **0.17** | **2** | **0.20** | **1.5** |
| BARE GROUND | 0.57 | 4.5 | 0.91 | 4 | 0.83 | 4 | 0.60 | 4 | 0.60 | 5 | 0.70 | 5 | 0.50 | 4 | 0.50 | 3 | 0.16 | 4 | 0.38 | 2 | 0.70 | 4 | 0.69 | 3 | 0.17 | 4 | 0.7 | 3 |

## Table (ii) continued (for Noda 21 and 33)

| | NODUM 21 | | | | NODUM 33 | | | | | NODUM 21 | | | | NODUM 33 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Original | | Present | | Original | | Present | | | Original | | Present | | Original | | Present | |
| Number of species recorded | 101 | | 82 | | 59 | | 72 | | | | | | | | | | |
| | F | D | F | D | F | D | F | D | | F | D | F | D | F | D | F | D |
| *Achillea millefolium* | 0.75 | 2 | 0.64 | 2 | | | 0.40 | 2 | *Botrychium lunaria* | 0.13 | 1 | 0.18 | 1 | | | | |
| ***Agrostis capillaris*** | **1.00** | **3.5** | **1.00** | **4** | **1.00** | **4** | **0.70** | **3** | *Brachythecium velutinum* | | | | | | | | |
| ***Agrostis stolonifera*** | **0.50** | **2** | **0.27** | **3** | **0.57** | **2** | **0.20** | **3.5** | ***Briza media*** | **0.88** | **4** | **0.82** | **3** | **0.71** | **3** | **0.40** | **2** |
| ***Agrostis vinealis*** | | | | | **0.29** | **1.5** | | | *Bryum caespiticium* | | | | | | | | |
| *Alchemilla glabra* | 0.50 | 2 | 0.45 | 3 | | | | | *Bryum capillare* | | | | | | | | |
| *Alchemilla filicaulis* | | | 0.18 | 2 | | | | | *Bryum pallens* | | | | | | | | |
| *Andreaea rothii* | | | | | | | | | *Bryum pseudotriquetrum* | 0.25 | 3 | | | 0.14 | 1 | | |
| ***Anemone nemorosa*** | | | | | | | | | *Calliergon cuspidatum* | 0.38 | 2 | 0.09 | 4 | | | | |
| *Aneura pinguis* | 0.13 | 1 | | | | | | | ***Calluna vulgaris*** | | | **0.18** | **2.5** | **0.29** | **5** | **0.10** | **2** |
| *Antennaria dioica* | 0.25 | 1 | 0.09 | 2 | | | | | ***Campanula rotundifolia*** | **0.88** | **4** | **0.64** | **2** | **0.57** | **3** | **0.40** | **2** |
| ***Anthoxanthum odoratum*** | **0.38** | **3** | **0.36** | **3** | **0.14** | **3** | **0.70** | **3** | *Campylium chrysophyllum* | | | | | | | | |
| *Anthyllis vulneraria* | | | | | | | | | *Campylium stellatum* | | | | | | | | |
| *Armeria maritima* | | | | | | | | | *Campylopus fragilis* | 0.13 | 2 | 0.09 | 2 | | | | |
| *Atrichum undulatum* | 0.38 | 3 | | | 0.14 | 2 | | | *Cardamine pratensis* | 0.25 | 1.5 | | | | | | |
| *Avenula pratensis* | | | | | | | | | *Carex binervis* | | | | | 0.14 | 2 | | |
| *Bacidia lignaria* | | | | | | | | | ***Carex capillaris*** | | | **0.18** | **1.5** | | | **0.20** | **2.5** |
| *Baeomyces rufus* | | | | | | | | | ***Carex caryophyllea*** | **1.00** | **3.5** | **0.73** | **2.5** | **0.57** | **2** | **0.50** | **2** |
| *Barbilophozia barbata* | | | | | | | 0.10 | 2 | *Carex ericetorum* | | | 0.18 | 1.5 | | | 0.10 | 2 |
| *Barbilophozia floerkei* | 0.25 | 1 | | | 0.29 | 3.5 | | | *Carex demissa* | | | | | | | | |
| *Barbula cylindrica* | | | | | | | | | *Carex flacca* | 0.75 | 3 | 0.64 | 4 | 0.14 | 4 | 0.10 | 2 |
| *Barbula reflexa* | 0.13 | 1 | | | | | | | ***Carex hostiana*** | | | | | **0.14** | **4** | | |
| *Barbula unguiculata* | | | | | | | | | *Carex lepidocarpa* | 0.13 | 2 | | | | | | |
| *Bellis perennis* | 0.63 | 2 | 0.55 | 2 | | | 0.10 | 1 | ***Carex panicea*** | **0.50** | **2.5** | **0.64** | **3** | **0.14** | **2** | **0.20** | **2** |

## Table (ii) continued

| | NODUM 21 | | | | NODUM 33 | | | | | NODUM 21 | | | | NODUM 33 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Original | | Present | | Original | | Present | | | Original | | Present | | Original | | Present | |
| | F | D | F | D | F | D | F | D | | F | D | F | D | F | D | F | D |
| ***Carex pilulifera*** | **0.50** | **2** | | | **0.71** | **3** | | | *Cololejeunea calcarea* | | | | | | | | |
| ***Carex pulicaris*** | **0.75** | **3** | **0.36** | **2** | | | **0.20** | **2.5** | ***Ctenidium molluscum*** | **0.25** | **2.5** | **0.45** | **1** | | | | |
| *Cephalozia bicuspidata* | | | | | | | | | ***Danthonia decumbens*** | **0.63** | **3** | **0.18** | **3.5** | **1.00** | **3** | **0.30** | **2** |
| *Cerastium fontanum* | 0.63 | 1 | 0.55 | 1 | | | 0.60 | 1 | *Deschampsia cespitosa* | 0.50 | 2 | 0.55 | 2.5 | 0.14 | 3 | 0.20 | 2 |
| *Cetraria islandica* | 0.13 | 1 | 0.09 | 1 | 0.29 | 2 | | | *Deschampsia flexuosa* | | | | | 0.14 | 1 | | |
| *Cirsium palustre* | | | 0.18 | 1.5 | | | | | *Dichodontium pellucidum* | 0.13 | 1 | | | | | | |
| *Cladonia ciliata* | | | | | | | 0.10 | 1 | *Dicranum bonjeanii* | 0.13 | 1 | | | | | 0.10 | 1 |
| ***Cladonia arbuscula*** | **0.25** | **4.5** | | | **0.71** | **5** | | | ***Dicranum scoparium*** | **0.63** | **2** | **0.27** | **1** | **1.00** | **3** | **0.30** | **1** |
| *Cladonia cariosa* | | | | | | | | | *Diplophyllum albicans* | 0.13 | 1 | | | | | | |
| *Cladonia chlorophaea* | | | | | | | | | ***Ditrichum flexicaule*** | | | **0.09** | **1** | | | | |
| *Cladonia coniocraea* | | | | | 0.14 | 2 | | | *Draba incana* | | | | | | | | |
| *Cladonia crispata* | | | | | | | | | *Drepanocladus revolvens* | | | | | | | | |
| *Cladonia furcata* | 0.13 | 2 | | | | | 0.20 | 1 | *Empetrum nigrum* | | | 0.09 | 2 | | | 0.10 | 1 |
| *Cladonia gracilis* | | | | | | | | | *Encalypta streptocarpa* | | | | | | | | |
| *Cladonia ochrochlora* | | | | | | | | | *Equisetum palustre* | | | | | | | 0.10 | 1 |
| *Cladonia pityrea* | | | | | | | | | *Equisetum variegatum* | | | | | | | | |
| ***Cladonia pocillum*** | **0.38** | **1** | | | | | | | ***Euphrasia rostkoviana*** | **1.00** | **2.5** | **0.82** | **2** | | | 0.40 | 1 |
| *Cladonia portentosa* | | | 0.18 | 1 | | | 0.40 | 3 | *Eurhynchium praelongum* | 0.13 | 2 | | | | | | |
| *Cladonia rangiformis* | 0.13 | 1 | | | | | 0.40 | 1.5 | ***Festuca ovina*** | **1.00** | **6.5** | **1.00** | **7** | **1.00** | **6** | **1.00** | **5.5** |
| ***Cladonia subrangiformis*** | **0.50** | **1.5** | | | **0.71** | **2** | | | *Festuca rubra* | | | | | 0.14 | 2 | 0.20 | 4 |
| *Cladonia subulata* | | | | | | | | | ***Fissidens adianthoides*** | **0.25** | **1.5** | **0.09** | **1** | | | | |
| *Cladonia uncialis* | 0.25 | 2.5 | | | 0.43 | 3 | 0.10 | 1 | *Fissidens cristatus* | | | | | | | | |
| *Climacium dendroides* | 0.13 | 2 | 0.09 | 1 | | | | | *Fissidens osmundoides* | | | | | | | | |
| ***Coelocaulon aculeatum*** | **0.38** | **1** | **0.09** | **1** | **0.14** | **1** | **0.10** | **1** | ***Frullania tamarisci*** | **0.13** | **2** | | | | | 0.10 | 1 |

## Table (ii) continued

| | NODUM 21 | | | | NODUM 33 | | | | | NODUM 21 | | | | NODUM 33 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Original | | Present | | Original | | Present | | | Original | | Present | | Original | | Present | |
| | F | D | F | D | F | D | F | D | | F | D | F | D | F | D | F | D |
| *Galium boreale* | 0.13 | 1 | 0.09 | 2 | | | 0.20 | 1 | ***Linum catharcticum*** | **0.50** | **1** | **0.73** | **1** | | | **0.20** | **1** |
| *Galium saxatile* | | | 0.09 | 3 | 0.86 | 5 | 1.00 | 3 | *Lophocolea bidentata* | 0.50 | 2 | | | 0.14 | 3 | | |
| ***Galium sterneri*** | **1.00** | **3** | **1.00** | **2** | | | **0.20** | **1** | *Lophozia ventricosa* | | | | | | | | |
| *Galium verum* | 0.13 | 1 | | | | | | | *Lotus corniculatus* | 0.38 | 4 | 0.55 | 3 | | | | |
| *Gentiana verna* | 0.38 | 2 | 0.36 | 1 | | | | | *Luzula campestris* | 0.75 | 2 | 0.36 | 2.5 | 0.71 | 3 | 0.80 | 3 |
| ***Gentianella amarella*** | **0.38** | **1** | **0.73** | **1.5** | | | **0.20** | **1.5** | *Minuartia verna* | 0.13 | 1 | 0.09 | 1 | | | | |
| *Geum rivale* | 0.18 | 1.5 | 0.13 | 1 | | | | | *Mnium hornum* | | | | | 0.14 | 4 | | |
| *Helianthemum nummularium* | | | 0.27 | 4 | | | | | *Molinia caerulea* | | | | | | | | |
| ***Hieracium pilosella*** | **0.38** | **3** | **0.64** | **2** | | | **0.10** | **3** | *Nardus stricta* | 0.25 | 1.5 | 0.18 | 4 | 0.43 | 7 | 0.40 | 3.5 |
| *Huperzia selago* | | | | | | | | | *Peltigera canina* | 0.38 | 1 | 0.09 | 1 | | | 0.10 | 1 |
| ***Hylocomium splendens*** | **0.75** | **2.5** | **0.55** | **2** | **0.14** | **3** | **0.90** | **1** | *Peltigera leucophlebia* | | | | | | | | |
| ***Hypnum cupressiforme* var. *lacunosum*** | **0.50** | **2** | **0.45** | **2** | | | **0.20** | **1.5** | *Peltigera praetextata* | | | | | | | | |
| *Hypnum cupressiforme* var. *resupinatum* | | | | | | | 0.10 | 1 | *Philonotis fontana* | 0.13 | 3 | | | | | | |
| ***Hypnum jutlandicum*** | **0.25** | **2** | **0.45** | **2** | **1.00** | **3** | **0.60** | **1** | *Pinguicula vulgaris* | | | | | | | | |
| *Hypochoeris radicata* | | | | | | | | | *Placynthiella uliginosa* | | | | | | | 0.10 | 2 |
| *Juncus acutiflorus* | | | | | | | | | ***Plagiochila asplenioides*** | **0.38** | **3** | | | **0.14** | **1** | | |
| *Juncus squarrosus* | | | | | | | 0.10 | 4 | *Plagiomnium rostratum* | 0.50 | 3 | | | | | 0.20 | 1 |
| *Kobresia simpliciuscula* | | | 0.09 | 1 | | | | | *Plagiomnium undulatum* | 0.13 | 3 | | | | | 0.10 | 1 |
| ***Koeleria macrantha*** | **0.75** | **4** | **1.00** | **3** | **0.14** | **2** | **0.30** | **3** | *Plantago lanceolata* | 0.75 | 4 | 1.00 | 4 | | | 0.10 | 2 |
| *Lathyrus montana* | | | | | | | | | *Plantago major* | 0.13 | 1 | | | | | | |
| *Leiocolea alpestris* | | | | | | | | | *Plantago major* | 0.13 | 1 | | | | | | |
| *Leontodon autumnalis* | 0.25 | 2.5 | | | | | | | *Plantago maritima* | 0.13 | 2 | 0.18 | 2 | 0.14 | 1 | | |

**Table (ii) continued**

| | NODUM 21 | | | | NODUM 33 | | | | | NODUM 21 | | | | NODUM 33 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Original | | Present | | Original | | Present | | | Original | | Present | | Original | | Present | |
| | F | D | F | D | F | D | F | D | | F | D | F | D | F | D | F | D |
| ***Pleurozium schreberi*** | **0.38** | **4** | **0.18** | **1.5** | **0.86** | **3.5** | **0.30** | **1** | *Rhytidium rugosum* | | | | | | | | |
| *Poa pratensis* | 0.13 | 3 | | | | | | | *Rumex acetosa* | | | | | | | 0.10 | 1 |
| *Pohlia nutans* | | | | | 0.14 | 1 | | | *Sanguisorba officinalis* | 0.13 | 2 | | | 0.14 | 1 | | |
| *Polygala amarella* | | | | | | | | | ***Scapania aspera*** | **0.25** | **1.5** | **0.09** | **2** | | | | |
| *Polygala serpyllifolia* | 0.13 | 1 | 0.09 | 1 | 0.14 | 2 | 0.30 | 2 | ***Selaginella selaginoides*** | **0.88** | **3** | **0.82** | **2** | | | **0.20** | **2** |
| *Polygonum viviparum* | 0.38 | 3 | 0.36 | 1 | | | | | ***Sesleria albicans*** | **0.63** | **2** | **0.45** | **4** | | | | |
| *Polytrichum commune* | | | | | 0.14 | 2 | | | *Solorina saccata* | | | 0.09 | 2 | | | | |
| *Polytrichum formosum* | 0.63 | 3 | 0.27 | 3 | 0.71 | 1 | 0.60 | 2 | *Succisa pratensis* | 0.13 | 1 | | | 0.14 | 1 | | |
| *Polytrichum juniperinum* | | | | | | | 0.30 | 2 | *Taraxacum officinale* | 0.13 | 2 | 0.45 | 1 | | | | |
| *Polytrichum piliiferum* | | | | | 0.14 | 1 | | | *Thalictrum alpinum* | | | | | | | | |
| *Potentilla crantzii* | | | | | | | | | *Thuidium delicatulum* | 0.13 | 5 | | | 0.14 | 2 | | |
| ***Potentilla erecta*** | **1.00** | **2.5** | **0.91** | **2** | **0.86** | **4** | **0.90** | **2** | *Thuidium philibertii* | 0.25 | 3 | | | | | | |
| *Primula farinosa* | | | | | | | | | *Thuidium tamariscinum* | 0.38 | 2 | 0.09 | 1 | | | | |
| *Prunella vulgaris* | 0.88 | 3 | 0.82 | 3 | 0.14 | 2 | 0.40 | 2 | ***Thymus praecox* subsp. *arcticus*** | **1.00** | **5.5** | **1.00** | **3** | | | **0.80** | **3** |
| *Pseudoscleropodium purum* | 0.75 | 2.5 | 0.64 | 2 | 0.14 | 2 | 0.20 | 1.5 | *Tofieldia pusilla* | | | | | | | | |
| *Ptilidium ciliare* | 0.25 | 1.5 | | | 0.43 | 1 | 0.10 | 1 | ***Tortella tortuosa*** | | | **0.27** | **1** | | | | |
| ***Racomitrium canescens*** | **0.38** | **2** | **0.18** | **1.5** | **0.14** | **1** | **0.10** | **1** | *Trichostomum brachydontium* | | | | | | | | |
| ***Racomitrium lanuginosum*** | **0.38** | **2** | **0.36** | **1.5** | **0.14** | **1** | **0.30** | **2** | *Trifolium repens* | 1.00 | 4 | 0.73 | 3 | 0.29 | 3.5 | 0.50 | 2 |
| *Ranunculus acris* | 0.75 | 1.5 | 0.45 | 2 | 0.14 | 2 | 0.10 | 2 | *Tritomaria quinquedentata* | 0.13 | 2 | | | | | | |
| *Rhodobryum roseum* | | | 0.09 | 2 | | | | | *Trollius europaeus* | | | | | | | | |
| ***Rhytidiadelphus loreus*** | | | | | | | | | *Vaccinium myrtillus* | | | | | 0.43 | 4 | 0.20 | 1.5 |
| *Rhytidiadelphus squarrosus* | 0.75 | 3.5 | 0.82 | 1 | 0.57 | 1.5 | 1.00 | 2 | *Veronica officinalis* | 0.13 | 2 | 0.09 | 3 | | | | |
| *Rhytidiadelphus triquetrus* | 0.13 | 3 | 0.36 | 1.5 | | | 0.20 | 1.5 | *Vicia orobus* | | | | | | | 0.10 | 2 |

**Table (ii) continued**

| | NODUM 21 | | | | NODUM 33 | | | |
|---|---|---|---|---|---|---|---|---|
| | Original | | Present | | Original | | Present | |
| | F | D | F | D | F | D | F | D |
| *Vicia sativa* | | | | | | | | |
| ***Viola lutea*** | **0.75** | **1** | **0.64** | **2** | **0.14** | **4** | **0.80** | **3** |
| *Viola riviniana* | 1.00 | 2.5 | 0.82 | 2 | 0.14 | 2 | 0.60 | 2 |
| *Viola riviniana* x *rupestris* | | | | | | | | |
| ***Viola rupestris*** | | | **0.09** | **3** | | | | |
| | | | | | | | | |
| BARE GROUND | | | 0.50 | 3 | | | 0.60 | 3 |

**Table (iii) Results from Mann-Whitney U-tests comparing raw Domin data between the present and original surveys for each species recorded. This table lists only the species for which there was no significant difference in frequency or abundance between surveys (Table 3.3. lists the species that have changed signficantly). U values are given, and changes in species frequency or abundance are indicated as new (N) i.e. the species was only recorded in the present survey; absent (A) i.e. the species was only recorded in the original survey; increased or decreased in frequency (+ or - respectively) or changing differently in terms of its frequency and abundance (+/- or -/+ respectively). See Table 3.1 for more details.**

**Forbs and shrubs**

| | NODUM 1 | | NODUM 2 | | NODUM 3 | | NODUM 4 | | NODUM 5 | | NODUM 6 | | NODUM 7 | | NODUM 21 | | NODUM 33 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change |
| *Achillea millefolium* | | | | | | | | | 170.0 | u | | | 63.0 | + | 54.0 | u | 49.0 | N |
| *Alchemilla filicaulis* subsp. *vestita* | | | | | | | | | 171.0 | N | | | | | 52.0 | N | | |
| *Alchemilla glabra* | | | | | | | 78.0 | A | 165.5 | + | 91.0 | A | | | 46.0 | + | | |
| *Antennaria dioica* | 40.0 | + | | | 29.5 | -/+ | 79.0 | - | 178.5 | + | 99.5 | + | 70.0 | A | 50.0 | + | | |
| *Anthyllis vulneraria* | | | 43.5 | + | | | | | | | 90.0 | + | | | | | | |
| *Armeria maritima* | | | | | | | | | | | | | 66.0 | N | | | | |
| *Bellis perennis* | | | 44.0 | N | | | | | 180.0 | +/- | 91.0 | N | 70.0 | A | 46.5 | u | 38.5 | N |
| *Botrychium lunaria* | | | | | | | 72.0 | u | 171.0 | N | | | | | 46.5 | u | | |
| *Cardamine pratensis* | | | | | | | 78.0 | A | | | | | | | 55.0 | A | | |
| *Cerastium fontanum* | | | | | | | 72.5 | - | 153.0 | + | | | | | 52.0 | u | 56.0 | N |
| *Cirsium palustre* | | | | | | | | | | | | | | | 52.0 | N | | |
| *Draba incana* | | | | | 30.0 | N | | | | | | | | | | | | |
| *Empetrum nigrum* | | | | | 27.5 | N | 72.5 | + | 159.0 | - | 85.0 | - | 65.0 | A | 48.0 | N | 38.5 | N |
| *Equisetum palustre* | | | | | | | | | | | 91.0 | N | | | | | 38.5 | N |
| *Equisetum variegatum* | | | | | | | | | | | 91.0 | A | | | | | | |
| *Galium boreale* | | | | | 27.5 | N | 84.0 | A | 160.0 | A | | | 64.0 | - | 45.0 | + | 42.0 | N |
| *Galium saxatile* | | | | | | | 104.0 | + | 160.0 | A | | | | | 48.0 | N | 56.0 | - |
| *Galium verum* | | | | | | | 78.0 | A | 162.0 | - | | | 68.0 | + | 55.0 | A | | |

**Table (iii) continued**

| | NODUM 1 | | NODUM 2 | | NODUM 3 | | NODUM 4 | | NODUM 5 | | NODUM 6 | | NODUM 7 | | NODUM 21 | | NODUM 33 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change |
| *Gentiana verna* | 42.0 | N | | | 42.0 | - | 96.5 | - | 165.5 | - | 105.0 | -/+ | 88.0 | - | 47.0 | - | | |
| *Geum rivale* | | | | | | | | | 163.0 | u | | | | | 47.0 | - | | |
| *Helianthemum nummularium* | 42.0 | -/+ | 40.5 | + | 27.0 | +/- | 79.0 | - | 155.0 | u | 86.0 | u | 80.0 | A | 56.0 | N | | |
| *Huperzia selago* | | | | | | | | | 160.0 | A | | | | | | | | |
| *Hypochoeris radicata* | | | | | | | | | | | | | 65.0 | A | | | | |
| *Lathyrus montanus* | | | | | 30.0 | A | 72.0 | u | | | | | | | | | | |
| *Leontodon autumnalis* | | | | | | | | | | | | | | | 55.0 | A | | |
| *Lotus corniculatus* | | | 45.0 | A | 27.5 | N | 88.5 | -/+ | 173.5 | + | 97.0 | + | 65.0 | A | 47.0 | - | | |
| *Minuartia verna* | 47.5 | + | 50.0 | + | 42.0 | + | | | 158.5 | u | 84.5 | u | 65.0 | A | 45.5 | u | | |
| *Pinguicula vulgaris* | | | | | | | | | 168.0 | A | | | 64.0 | + | | | | |
| *Plantago lanceolata* | 42.0 | N | 44.0 | N | 32.5 | N | 84.0 | A | 159.0 | + | 92.0 | + | 64.5 | + | 46.0 | + | 38.5 | N |
| *Plantago major* | | | | | | | | | | | | | | | 49.5 | A | | |
| *Plantago maritima* | 41.5 | + | 45.0 | + | 27.0 | u | 84.0 | A | 198.0 | - | 97.5 | u | 63.0 | -/+ | 46.5 | u | 40.0 | A |
| *Pohlia nutans* | | | | | | | | | | | | | | | | | 40.0 | A |
| *Polygala amarella* | | | | | 30.0 | A | | | 168.0 | A | 123.5 | A | | | | | | |
| *Polygala serpyllifolia* | | | | | | | 95.0 | +/- | 168.5 | - | 91.0 | N | 65.0 | A | 45.5 | u | 40.0 | u |
| *Polygonum viviparum* | | | 44.0 | N | 27.0 | + | 84.5 | u | 180.0 | - | 94.0 | + | 81.5 | - | 48.0 | - | | |
| *Potentilla crantzii* | | | | | 30.0 | A | 96.0 | A | 192.0 | A | 104.0 | A | | | | | | |
| *Primula farinosa* | 42.0 | N | 45.0 | A | 27.5 | N | | | | | | | 76.0 | - | | | | |
| *Prunella vulgaris* | | | 44.0 | N | 27.5 | u | 78.0 | A | 154.5 | u | 97.5 | A | 88.0 | + | 47.0 | - | 43.5 | u |
| *Ranunculus acris* | | | | | | | 89.0 | - | 153.0 | - | 91.0 | N | | | 57.0 | -/+ | 36.5 | u |
| *Rumex acetosa* | | | | | | | | | | | | | | | | | 38.5 | N |
| *Sanguisorba officinalis* | | | | | | | 96.0 | A | | | | | | | 49.5 | A | 40.0 | A |
| *Succisa pratensis* | | | | | 27.5 | N | 73.0 | + | 157.0 | u | 86.5 | + | 64.0 | + | 49.5 | A | 40.0 | A |
| *Taraxacum officinale* | | | 45.0 | A | 27.5 | N | 78.0 | N | 154.5 | - | | | 65.0 | A | 57.0 | +/- | | |

**Table (iii) continued**

| | NODUM 1 | | NODUM 2 | | NODUM 3 | | NODUM 4 | | NODUM 5 | | NODUM 6 | | NODUM 7 | | NODUM 21 | | NODUM 33 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change |
| *Thalictrum alpinum* | | | | | | | 85.0 | - | 161.5 | N | 97.5 | N | 63.5 | - | | | | |
| *Tofieldia pusilla* | | | | | | | | | | | | | 61.0 | - | | | | |
| *Trifolium repens* | | | 44.0 | N | 30.0 | A | 78.0 | N | 168.5 | u | | | 66.0 | N | 69.0 | - | 38.5 | +/- |
| *Trollius europaeus* | | | | | | | 84.0 | A | | | | | 70.0 | A | | | | |
| *Vaccinium myrtillus* | | | | | | | | | | | | | | | | | 46.0 | - |
| *Veronica officinalis* | | | | | | | | | 159.0 | - | | | | | 45.0 | + | | |
| *Vicia orobus* | | | | | | | | | | | | | | | | | 38.5 | N |
| *Vicia sativa* | | | | | | | | | 161.5 | N | | | | | | | | |
| *Viola riviniana* | 47.5 | + | 52.0 | N | 28.0 | u | 80.0 | u | 170.5 | u | 112.5 | - | 60.5 | u | 54.5 | - | 50.5 | + |
| *Viola riviniana* x *rupestris* | 44.0 | A | | | | | | | 160.0 | A | | | | | | | | |
| **Grasses, sedges and rushes** | | | | | | | | | | | | | | | | | | |
| *Avenula pratensis* | 47.0 | - | 44.0 | + | | | 84.0 | A | 156.0 | u | 91.0 | A | 85.0 | A | | | | |
| *Carex binervis* | | | | | | | | | | | | | | | | | 40.0 | A |
| *Carex demissa* | | | | | | | 78.0 | A | 160.0 | A | | | | | | | | |
| *Carex ericetorum* | 60.5 | - | 43.5 | - | | | 78.0 | A | 171.0 | - | | | 78.0 | N | 52.0 | N | 38.5 | N |
| *Carex flacca* | 45.0 | u | 54.0 | + | 27.0 | + | 75.5 | u | 166.5 | -/+ | 106.5 | + | 64.0 | + | 46.0 | + | 37.0 | - |
| *Carex lepidocarpa* | | | | | | | | | 160.0 | | | | 60.5 | + | 49.5 | A | | |
| *Deschampsia cespitosa* | | | | | | | | | | | 91.0 | A | 70.0 | A | 47.5 | + | 36.0 | - |
| *Deschampsia flexuosa* | | | | | | | | | | | | | | | | | 40.0 | A |
| *Festuca rubra* | | | | | | | | | | | | | 65.0 | A | | | 38.0 | + |
| *Juncus acutiflorus* | | | | | | | | | | | | | 66.0 | N | | | | |
| *Juncus squarrosus* | | | | | | | | | 160.0 | A | | | | | | | 38.5 | N |
| *Kobresia simpliciuscula* | 39.5 | + | 52.0 | N | 32.5 | N | 72.0 | u | 174.0 | + | 88.0 | + | 83.5 | - | 48.0 | N | | |
| *Luzula campestris* | | | | | | | 78.0 | A | 168.5 | + | | | | | 58.0 | -/+ | 37.5 | u |

**Table (iii) continued**

| | NODUM 1 | | NODUM 2 | | NODUM 3 | | NODUM 4 | | NODUM 5 | | NODUM 6 | | NODUM 7 | | NODUM 21 | | NODUM 33 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change |
| *Molinia caerulea* | | | | | | | | | | | | | 78.0 | N | | | | |
| *Nardus stricta* | | | | | | | 78.0 | A | | | | | | | 45.0 | + | 37.5 | - |
| *Poa pratensis* | | | | | | | | | | | | | | | 49.5 | A | | |

**Mosses**

| | NODUM 1 | | NODUM 2 | | NODUM 3 | | NODUM 4 | | NODUM 5 | | NODUM 6 | | NODUM 7 | | NODUM 21 | | NODUM 33 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Andreaea rothii* | | | | | | | | | | | | | 66.0 | N | | | | |
| *Atrichum undulatum* | | | | | | | | | 160.0 | A | | | | | 60.5 | A | 40.0 | A |
| *Barbilophozia barbata* | | | | | | | | | 168.0 | A | 91.0 | A | 65.0 | A | | | 38.5 | N |
| *Barbula cylindrica* | 42.0 | N | | | | | | | | | | | | | | | | |
| *Barbula reflexa* | | | 45.0 | A | 30.0 | A | | | | | | | | | 49.5 | A | | |
| *Barbula unguiculata* | | | | | | | 78.0 | A | | | | | | | | | | |
| *Brachythecium velutinum* | | | | | | | | | | | | | 65.0 | A | | | | |
| *Bryum caespiticium* | | | | | | | 78.0 | A | | | | | 66.0 | N | | | | |
| *Bryum capillare* | | | | | 27.5 | N | | | | | | | 65.0 | A | | | | |
| *Bryum pallens* | | | | | | | | | 153.5 | u | | | 65.0 | A | | | | |
| *Bryum pseudotriquetrum* | | | 50.0 | A | | | 78.0 | A | 160.0 | A | | | 70.0 | A | 55.0 | A | 40.0 | A |
| *Calliergon cuspidatum* | | | 50.0 | A | | | | | 176.0 | A | | | 80.0 | - | 55.0 | -/+ | | |
| *Campylium chrysophyllum* | | | | | 30.0 | A | | | 168.0 | A | 91.0 | A | 70.0 | A | | | | |
| *Campylium stellatum* | | | | | | | | | | | | | 70.0 | A | | | | |
| *Campylopus fragilis* | 49.0 | N | 48.0 | N | 32.5 | N | 78.0 | A | | | 91.0 | u | 68.0 | + | 45.5 | u | | |
| *Climacium dendroides* | | | | | | | | | 160.0 | A | | | | | 46.0 | - | | |
| *Dichodontium pellucidum* | | | | | | | | | | | | | | | 49.5 | A | | |
| *Dicranum bonjeanii* | | | | | | | 104.0 | - | 200.0 | A | 104.0 | A | 65.0 | A | 49.5 | A | 38.5 | N |
| *Drepanocladus revolvens* | | | | | | | | | | | | | 75.0 | A | | | | |
| *Encalypta streptocarpa* | 44.0 | A | 43.0 | u | | | | | 161.5 | N | | | | | | | | |

**Table (iii) continued**

| | NODUM 1 | | NODUM 2 | | NODUM 3 | | NODUM 4 | | NODUM 5 | | NODUM 6 | | NODUM 7 | | NODUM 21 | | NODUM 33 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change |
| *Eurhynchium praelongum* | | | | | | | | | | | | | | | 49.5 | A | | |
| *Fissidens cristatus* | | | | | | | | | 161.5 | N | | | | | | | | |
| *Fissidens osmundoides* | | | | | | | | | 160.0 | A | | | | | | | | |
| *Hypnum cupressiforme* var. *resupinatum* | 45.5 | N | | | 27.5 | N | | | | | | | 66.0 | N | | | 38.5 | N |
| *Mnium hornum* | | | | | | | 78.0 | A | | | | | | | | | 40.0 | A |
| *Philonotis fontana* | | | | | | | | | | | | | | | 49.5 | A | | |
| *Plagiomnium rostratum* | | | | | 27.5 | N | 84.0 | A | 167.0 | u | 91.0 | N | 65.0 | A | 66.0 | A | 42.0 | N |
| *Plagiomnium undulatum* | | | | | | | | | 168.0 | A | | | | | | | 38.5 | N |
| *Polytrichum piliferum* | | | | | | | | | 160.0 | A | | | | | | | 40.0 | A |
| *Polytrichum commune* | | | | | | | | | | | | | | | | | 40.0 | A |
| *Polytrichum formosum* | | | | | | | 80.0 | - | 190.0 | - | | | | | 60.5 | - | 39.0 | + |
| *Polytrichum juniperinum* | | | | | | | 78.0 | N | 160.0 | A | | | | | | | 45.5 | N |
| *Pseudoscleropodium purum* | 42.0 | N | 44.0 | N | 26.5 | u | 76.0 | - | 177.0 | - | 97.0 | u | 65.5 | + | 56.5 | - | 36.5 | - |
| *Rhodobryum roseum* | | | | | | | | | 171.0 | N | | | | | 48.0 | N | | |
| *Rhytidiadelphus squarrosus* | 40.5 | u | 44.0 | N | 30.0 | N | 80.5 | + | 193.0 | - | 89.5 | - | 65.0 | A | 52.5 | - | 51.5 | + |
| *Rhytidiadelphus triquetrus* | | | 44.0 | N | 27.5 | N | 78.0 | A | 160.0 | + | | | 76.0 | + | 52.5 | +/- | 42.0 | N |
| *Rhytidium rugosum* | 44.0 | A | 56.0 | - | | | | | | | | | | | | | | |
| *Thuidium delicatulum* | | | | | | | | | | | | | 65.0 | A | 49.5 | A | 40.0 | A |
| *Thuidium philibertii* | | | | | | | | | 168.0 | A | | | 65.0 | A | 55.0 | A | | |
| *Thuidium tamariscinum* | | | | | | | 78.0 | A | 191.5 | - | 91.0 | A | 65.0 | A | 57.5 | - | | |
| *Trichostomium brachydontium* | 44.0 | A | | | | | | | | | | | | | | | | |
| *Tritomaria quinquedentata* | | | | | | | | | 160.0 | A | | | | | 49.5 | A | | |

**Table (iii) continued**

| | NODUM 1 | | NODUM 2 | | NODUM 3 | | NODUM 4 | | NODUM 5 | | NODUM 6 | | NODUM 7 | | NODUM 21 | | NODUM 33 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change |
| **Liverworts** | | | | | | | | | | | | | | | | | | |
| *Aneura pinguis* | | | | | | | | | | | | | | | 49.5 | A | | |
| *Barbilophozia floerkei* | | | | | | | 78.0 | A | 176.0 | A | | | | | 55.0 | A | 45.0 | A |
| *Cephalozia bicuspidata* | | | | | | | | | | | | | 65.0 | A | | | | |
| *Cololejeunea calcarea* | | | | | | | | | | | | | 65.0 | A | | | | |
| *Diplophyllum albicans* | | | | | | | | | | | | | | | 49.5 | A | | |
| *Leiocolea alpestris* | | | | | | | | | | | | | 65.0 | A | | | | |
| *Lophocolea bidentata* | | | | | | | 84.0 | A | 184.0 | A | | | 65.0 | A | 66.0 | A | 40.0 | A |
| *Lophozia ventricosa* | | | | | | | | | | | 91.0 | A | | | | | | |
| *Ptilidium ciliare* | | | | | | | 84.0 | A | 168.0 | A | | | | | 55.0 | A | 47.0 | - |
| **Lichens** | | | | | | | | | | | | | | | | | | |
| *Bacidia lignaria* | | | | | | | | | 160.0 | A | 91.0 | A | 65.0 | A | | | | |
| *Baeomyces rufus* | | | | | 28.0 | - | 84.0 | A | | | | | | | | | | |
| *Cetraria islandica* | 46.0 | - | 59.0 | - | 41.0 | - | 90.0 | - | 195.0 | -/+ | 122.0 | - | 90.0 | A | 45.5 | u | 45.0 | A |
| *Cladonia ciliata* | | | | | | | | | | | | | | | | | 38.5 | N |
| *Cladonia cariosa* | | | | | | | | | | | | | 65.0 | A | | | | |
| *Cladonia chlorophaea* | | | | | | | 72.5 | + | | | 91.0 | A | | | | | | |
| *Cladonia coniocraea* | | | | | 27.5 | N | 78.0 | u | | | | | | | | | 40.0 | A |
| *Cladonia crispata* | | | | | | | | | 161.5 | N | | | | | | | | |
| *Cladonia furcata* | 42.0 | N | 48.0 | N | 38.0 | + | 72.5 | - | 190.0 | N | 110.5 | N | 66.0 | N | 49.5 | A | 42.0 | N |
| *Cladonia gracilis* | | | | | | | 78.0 | A | | | | | | | | | | |
| *Cladonia ochrochlora* | | | | | | | | | 160.0 | A | 91.0 | A | 65.0 | A | | | | |
| *Cladonia pityrea* | | | 48.0 | N | | | | | | | | | | | | | | |

**Table (iii) continued**

| | NODUM 1 | | NODUM 2 | | NODUM 3 | | NODUM 4 | | NODUM 5 | | NODUM 6 | | NODUM 7 | | NODUM 21 | | NODUM 33 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change | value of U | change |
| *Cladonia portentosa* | | | | | 27.5 | N | 96.0 | N | 180.5 | N | 85.0 | - | | | 52.0 | N | 49.0 | N |
| *Cladonia rangiformis* | 42.0 | N | 44.0 | N | 27.5 | u | 78.0 | N | 153.0 | - | 90.0 | - | 61.5 | + | 49.5 | A | 49.0 | N |
| *Cladonia subulata* | | | | | 27.5 | N | | | | | | | | | | | | |
| *Cladonia uncialis* | 42.0 | N | | | | | | | 162.5 | - | | | | | 55.0 | A | 47.5 | - |
| *Peltigera canina* | 42.0 | N | 48.0 | N | 35.0 | N | | | 161.0 | + | 84.5 | u | | | 57.0 | - | 38.5 | N |
| *Peltigera leucophlebia* | | | | | 30.0 | A | 78.0 | A | 184.0 | A | 97.5 | A | | | | | | |
| *Peltigera praetextata* | | | | | | | | | 160.0 | A | | | 65.0 | A | | | | |
| *Placynthiella uliginosa* | | | | | | | | | | | | | | | | | 38.5 | N |
| *Solorina saccata* | 42.0 | N | 45.0 | A | 27.5 | N | | | 171.0 | N | | | | | 48.0 | N | | |
| BARE GROUND | 47.5 | | 50.0 | | 27.5 | | 90.9 | | 176.0 | | 111.5 | | 87.0 | | 68.0 | | 56.0 | |

# Appendix C

**Table (i) Mean Nuclear DNA content for families representing the species found in the two surveys (Grime *et al.*, 1988).**

| Family | Mean Nuclear DNA (pg) | Standard Deviation | number of species in each family recorded |
|---|---|---|---|
| Campanulaceae | (5.3) | - | 1 |
| Caryophyllaceae | 4.35 | 2.19 | 2 |
| Cistaceae | (4.5) | - | 1 |
| Compositae | 5.85 | 5.05 | 6 |
| Cruciferae | (3.3) | - | 1 |
| Cyperaceae | 1.40 | 0.72 | 3 |
| Dipsacaceae | (5.50) | - | 1 |
| Equisetaceae | (25) | - | 1 |
| Gramineae | 11.54 | 7.89 | 15 |
| Juncaceae | 1.15 | 0.07 | 2 |
| Labiatae | 2.05 | 1.06 | 2 |
| Leguminosae | 7.27 | 8.01 | 3 |
| Linaceae | (1.2) | - | 1 |
| Plantaginaceae | 2.05 | 0.49 | 2 |
| Polygonaceae | (3.3) | - | 1 |
| Ranunculaceae | 24.4 | 19.37 | 2 |
| Rubiaceae | 2.93 | 0.95 | 3 |
| Violaceae | (2.7) | - | 1 |

**Reaction value (Ellenberg, 1988)**

1. Indicators of extreme acidity, never found on weakly acid or alkaline soils
2. between points 1 and 3 on the scale
3. Acid indicators, mainly on acid soils but can also be found where there is a neutral reaction
4. between 3 and 5
5. Indicators of fairly acid soils, only occasionally found in more acid, or in neutral to slightly alkaline situations
6. between 5 and 7
7. Indicators of weakly acid to weakly basic conditions. Never found on very acid soils
8. between 7 and 9, i.e. mostly seen on limestone or chalk
9. Basic reaction and lime indicators, always found on calcareous soils

**Nitrogen value (Ellenberg, 1988)**

1. Indicators of sites poor in available nitrogen
2. between 1 and 3
3. More often found on nitrogen-deficient soils than on richer ones
4. between 3 and 5
5. Indicators of sites with average nitrogen availability, seldom found on either poorer or richer soils
6. between 5 and 7
7. More often found in places rich in available nitrogen than in poor or average situations
8. between 7 and 9
9. In extremely rich situations (cattle resting places; indicators of pollution)

x on either scale indicates a species of wide ecological amplitude or one with different behaviour in different parts of Europe.

**Table (ii) Ecological and physiological traits for all species recorded in either survey in the nine noda under study. See accompanying notes at the end of the table. See also text (Section 4.1) for data sources.**

| | Predominant change across the noda [1] | Floristic element number [2] | Longevity annual (A) biennial (B) perennial (P) | Regenerative strategy [3] | Leaf phenology [4] | Flowering time and duration [5] | C-S-R strategy [6] | nDNA content | Standardised nDNA content [7] | Reaction value [8] | Nitrogen value [9] |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Achillea millefolium* | | 55 | P | V,?S | Ea | Jun 3 | CR/CSR | 15.3 | 1.87 | x | 5 |
| *Agrostis capillaris* | + | 54 | P | V B | Ea | Jun 3 | CSR | 7.1 | -0.56 | 3 | 3 |
| *Agrostis stolonifera* | - | 66 | P | V B | Ea | Jul 2 | CR | 7 | -0.58 | x | 5 |
| *Agrostis vinealis* | + | 73 | P | B V | Ea | Jun 3 | CSR | 6.9 | -0.59 | 3 | 1 |
| *Alchemilla filicaulis* subsp. *vestita* | | 43 | P | ? | | | | | | | |
| *Alchemilla glabra* | | 53 | P | ? | Ea | Jun 4 | | | | x | 6 |
| *Andreaea rothii* | | 53 | | | | | | | | I | |
| *Anemone nemorosa* | + | 74 | P | V | Sv | Mar 3 | S/SR | 38.1 | 0.71 | I | x |
| *Aneura pinguis* | | 36 | | | | | | | | | |
| *Antennaria dioica* | | 55 | P | | | | | | | 3 | 3 |
| *Anthoxanthum odoratum* | + | 64 | P | S B | Ea | Apr 3 | SR/CSR | 11.8 | 0.03 | 5 | x |
| *Anthyllis vulneraria* | | 53 | P | ?B | Ea | Jun 4 | S/SR | | | 8 | 3 |
| *Armeria maritima* | | 36 | P | | | | | | | 5 | 3 |
| *Atrichum undulatum* | | 56 | | | | | | | | I | |
| *Avenula pratensis* | | 73 | P | S | Ea | Jun 1 | S/CS | 35.9 | 3.09 | | |
| *Bacidia lignaria* | | | | | | | | | | A | |
| *Baeomyces rufus* | | | | | | | | | | A | |
| *Barbilophozia barbata* | | 46 | | | | | | | | I | |

**Table (ii) continued**

| | Predominant change across the noda | Floristic element number | Longevity | Regenerative strategy | Leaf phenology | Flowering time and duration | C-S-R strategy | nDNA content | Standardised nDNA content | Reaction value | Nitrogen value |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Barbilophozia floerkei* | | 46 | | | | | | | | I | |
| *Barbula cylindrica* | | 85 | | | | | | | | I | |
| *Barbula reflexa* | | 53 | | | | | | | | I | |
| *Barbula unguiculata* | | 66 | | | | | | | | I | |
| *Bellis perennis* | | 73 | P | V | Ea | Mar 12 | R/CSR | 3.9 | -0.39 | x | 5 |
| *Botrychium lunaria* | | 56 | P | | | | | | | x | 2 |
| *Brachythecium velutinum* | | 76 | | | | | | | | I | |
| *Briza media* | - | 73 | P | S V | Ea | Jun 2 | S | 16.9 | 0.68 | x | 2 |
| *Bryum caespiticium* | | 56 | | | | | | | | I | |
| *Bryum pseudotriquetrum* | | 36 | | | | | | | | I | |
| *Calliergon cuspidatum* | | 76 | | | | | | | | I | |
| *Calluna vulgaris* | + | 53 | P | S | Ea | Aug 2 | SC | | | 1 | 1 |
| *Campanula rotundifolia* | - | 56 | P | V B | Ea | Jul 3 | S | 5.3 | | x | 2 |
| *Campylium chrysophyllum* | | 56 | | | | | | | | C | |
| *Campylium stellatum* | | 56 | | | | | | | | I | |
| *Campylopus fragilis* | | 72 | | | | | | | | I | |
| *Cardamine pratensis* | | 36 | P | (V)?B | Ea | Apr 3 | R/CSR | 3.3 | 0.82 | x | x |
| *Carex binervis* | | 71 | | VB | | | S | | | | |
| *Carex capillaris* | - | 26 | P | | | | | | | 8 | 2 |
| *Carex caryophyllea* | - | 74 | P | V | Ea | Apr 2 | S | 1.6 | 0.28 | x | 2 |
| *Carex demissa* | | | P | B | Ea | Jun 1 | S | | | | |
| *Carex ericetorum* | | 54 | P | | | | | | | x | 2 |
| *Carex flacca* | | 83 | P | V B | Ea | May 2 | S | 0.6 | -1.11 | 8 | x |
| *Carex hostiana* | - | 73 | P | | Ea | Jun 1 | | | | 6 | 2 |

**Table (ii) continued**

| | Predominant change across the noda | Floristic element number | Longevity | Regenerative strategy | Leaf phenology | Flowering time and duration | C-S-R strategy | nDNA content | Standardised nDNA content | Reaction value | Nitrogen value |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Carex lepidocarpa* | | 73 | P | ? | | | S | | | | |
| *Carex panicea* | +/- | 53 | P | V ?S | Ea | May 2 | S | 2 | 0.83 | x | 3 |
| *Carex pilulifera* | - | 73 | P | B V | Ea | May 2 | S | | | 3 | 5 |
| *Carex pulicaris* | - | 72 | P | | | | | | | x | ? |
| *Cephalozia bicuspidata* | | 56 | | | | | | | | A | |
| *Cerastium fontanum* | | 54 | P | B (V) | Ea | Apr 6 | R/CSR | 5.9 | 0.71 | 3 | 6 |
| *Cetraria islandica* | | | | | | | | | | A | |
| *Cirsium palustre* | | 54 | P | W B | Ea | Jul 3 | CSR | 2.7 | -0.62 | 4 | 3 |
| *Cladonia arbuscula* | - | | | | | | | | | A | |
| *Cladonia cariosa* | | | | | | | | | | C | |
| *Cladonia chlorophaea* | | | | | | | | | | A | |
| *Cladonia ciliata* | | | | | | | | | | A | |
| *Cladonia coniocraea* | | | | | | | | | | I | |
| *Cladonia crispata* | | | | | | | | | | A | |
| *Cladonia furcata* | | | | | | | | | | C | |
| *Cladonia gracilis* | | | | | | | | | | I | |
| *Cladonia ochrochlora* | | | | | | | | | | I | |
| *Cladonia pityrea* | | | | | | | | | | I | |
| *Cladonia pocillum* | - | | | | | | | | | C | |
| *Cladonia portentosa* | | | | | | | | | | A | |
| *Cladonia rangiformis* | | | | | | | | | | I | |
| *Cladonia subrangiformis* | - | | | | | | | | | C | |
| *Cladonia subulata* | | | | | | | | | | I | |
| *Cladonia uncialis* | | | | | | | | | | A | |

**Table (ii) continued**

| | Predominant change across the noda | Floristic element number | Longevity | Regenerative strategy | Leaf phenology | Flowering time and duration | C-S-R strategy | nDNA content | Standardised nDNA content | Reaction value | Nitrogen value |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Climacium dendroides* | | 36 | | | | | | | | I | |
| *Coelocaulon aculeatum* | - | | | | | | | | | A | |
| *Cololejeuna calcarea* | | 52 | | | | | | | | | |
| *Ctenidium molluscum* | - | 53 | | | | | | | | C | |
| *Danthonia decumbens* | - | 73 | P | B | Ea | Jul 1 | S | 5.9 | -0.71 | 3 | 2 |
| *Deschampsia cespitosa* | | 36 | P | S B V | Ea | Jun 3 | S/CSR | 18 | 0.82 | x | 3 |
| *Deschampsia flexuosa* | | 53 | P | V S | Ea | Jun 2 | S/CS | 11 | -0.07 | | |
| *Dicranum bonjeani* | | 56 | | | | | | | | I | |
| *Dicranum scoparium* | +/- | 36 | | | | | | | | I | |
| *Diplophyllum albicans* | | 52 | | | | | | | | | |
| *Ditrichum flexicaule* | - | 66 | | | | | | | | C | |
| *Draba incana* | | 23 | P | | | | | | | | |
| *Drepanocladus revolvens* | | 26 | | | | | | | | I | |
| *Empetrum nigrum* | | 26 | P | V S ?B | Ea | Apr 2 | SC | | | x | 2 |
| *Encalypta streptocarpa* | | 55 | | | | | | | | C | |
| *Equisetum palustre* | | 56 | P | V W | | | CR/CSR | 25 | -1.05 | x | 3 |
| *Equisetum variegatum* | | 26 | P | | | | | | | | |
| *Euphrasia rostkoviana* | - | 53 | A | S | Sa | Jun 4 | SR | | | x | 3 |
| *Eurhynchium praelongum* | | 73 | | | | | | | | | |
| *Festuca ovina* | + | 55 | P | S V | Ea | May 3 | S | 9.5 | -0.26 | 3 | x |
| *Festuca rubra* | | 36 | P | V S | Ea | May 3 | CSR | 13.9 | 0.30 | x | x |
| *Fissidens adianthoides* | - | 56 | | | | | | | | I | |
| *Fissidens cristatus* | | 73 | | | | | | | | I | |
| *Fissidens osmundoides* | | 26 | | | | | | | | I | |

**Table (ii) continued**

| | Predominant change across the noda | Floristic element number | Longevity | Regenerative strategy | Leaf phenology | Flowering time and duration | C-S-R strategy | nDNA content | Standardised nDNA content | Reaction value | Nitrogen value |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Frullania tamarisci* | - | 52 | | | | | | | | I | |
| *Galium boreale* | | 56 | P | | | | | | | 8 | 2 |
| *Galium saxatile* | | 72 | P | V B | Ea | Jun 3 | S | 2.9 | -0.04 | C | |
| *Galium sterneri* | - | 42 | P | V? B | Ea | Jun 2 | S | 2 | -0.98 | 4 | 2 |
| *Galium verum* | | 55 | P | V B | Ea | Jul 2 | CS/CSR | 3.9 | 1.02 | 7 | 3 |
| *Gentiana verna* | | 13 | P | | | | | | | 7 | 2 |
| *Gentianella amarella* | + | 56 | B | B | Sa | Aug 3 | SR | | | | |
| *Geum rivale* | | 54 | P | S | | | S/CSR | | | x | 4 |
| *Helianthemum nummularium* | | 73 | P | B | Ea | Jun 2 | S | 4.5 | | 7 | 1 |
| *Hieracium pilosella* | + | 73 | P | V W | Ea | May 2 | S/CSR | 7.9 | 0.41 | x | 2 |
| *Huperzia selago* | | 26 | | | | | | | | | |
| *Hylocomium splendens* | +/- | 36 | | | | | | | | A | |
| *Hypnum cupressiforme* var. *lacunosum* | - | 66 | | | | | | | | C | |
| *Hypnum cupressiforme* var. *resupinatum* | | 66 | | | | | | | | I | |
| *Hypnum jutlandicum* | - | 72 | | | | | | | | A | |
| *Hypochoeris radicata* | | 83 | P | V W | Ep | Jun 4 | CSR | | | 4 | 3 |
| *Juncus acutiflorus* | | 73 | P | V B | Sa | Jul 3 | SC | | | 5 | 3 |
| *Juncus squarrosus* | | 72 | P | V B | Ea | Jun 2 | S | 1.1 | -0.71 | 1 | 1 |
| *Kobresia simpliciuscula* | | 16 | P | | | | | | | | |
| *Koeleria macrantha* | - | 76 | P | S | Ea | Jun 2 | S | 9.3 | -0.28 | 8 | 2 |
| *Lathyrus montanus* | | | P | V ?B | Sa | Apr 4 | S/CSR | 16.5 | 1.15 | 9 | 3 |

**Table (ii) continued**

| | Predominant change across the noda | Floristic element number | Longevity | Regenerative strategy | Leaf phenology | Flowering time and duration | C-S-R strategy | nDNA content | Standardised nDNA content | Reaction value | Nitrogen value |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Leiocolea alpestris* | | 26 | | | | | | | | | |
| *Leontodon autumnalis* | | 53 | P | W B | Ea | Jun 5 | R/CSR | 2.7 | -0.62 | | |
| *Linum catharticum* | - | 73 | B | S B | Ea | Jun 4 | SR | 1.2 | | x | 1 |
| *Lophocolea bidentata* | | 73 | | | | | | | | I | |
| *Lophozia ventricosa* | | 53 | | | | | | | | A | |
| *Lotus corniculatus* | | 85 | P | B | Sa | Jun 4 | S/CSR | 2.2 | -0.63 | 7 | 3 |
| *Luzula campestris* | | 73 | P | V B | Ea | Mar 4 | S/CSR | 1.2 | 0.71 | 3 | 2 |
| *Minuartia verna* | | 45 | P | V B | Ea | May 5 | S | 2.8 | -0.71 | x | 1 |
| *Mnium hornum* | | 73 | | | | | | | | A | |
| *Molinia caerulea* | | 54 | P | V?B | Sa | Jun 3 | SC | 4.9 | -0.84 | x | 2 |
| *Nardus stricta* | | 53 | P | V S | Ea | Jun 3 | S | 4.2 | -0.93 | 2 | 2 |
| *Peltigera canina* | | | | | | | | | | C | |
| *Peltigera leucophlebia* | | | | | | | | | | C | |
| *Peltigera praetextata* | | | | | | | | | | I | |
| *Philonotis fontana* | | 66 | | | | | | | | | |
| *Pinguicula vulgaris* | | 46 | P | | | | | | | 7 | 2 |
| *Placynthiella uliginosa* | | | | | | | | | | A | |
| *Plagiochila asplenioides* | - | 73 | | | | | | | | C | |
| *Plagiomnium rostratum* | | 53 | | | | | | | | I | |
| *Plagiomnium undulatum* | | 73 | | | | | | | | I | |
| *Plantago lanceolata* | | 84 | P | BV | Ea | Apr 5 | CSR | 2.4 | 0.71 | x | x |
| *Plantago major* | | 65 | P | B | Ep | Jun 4 | R/CSR | 1.7 | -0.71 | x | 6 |
| *Plantago maritima* | | 34 | P | | | | | | | 8 | x |
| *Pleurozium schreberi* | - | 56 | | | | | | | | A | |

**Table (ii) continued**

| | Predominant change across the noda | Floristic element number | Longevity | Regenerative strategy | Leaf phenology | Flowering time and duration | C-S-R strategy | nDNA content | Standardised nDNA content | Reaction value | Nitrogen value |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Poa pratensis* | | 66 | P | V ?B | Ea | May 3 | CSR | 10.8 | -0.09 | x | 6 |
| *Pohlia nutans* | | | | | | | | | | | |
| *Polygala amarella* | | 53 | P | | | | | | | 8 | 2 |
| *Polygala serpyllifolia* | | 72 | P | | | | S | | | 2 | 2 |
| *Polygonum viviparum* | | | P | ?S | | | | | | 3 | x |
| *Polytrichum commune* | | 36 | | | | | | | | A | |
| *Polytrichum formosum* | | 56 | | | | | | | | A | |
| *Polytrichum juniperinum* | | 36 | | | | | | | | A | |
| *Polytrichum piliferum* | | 36 | | | | | | | | A | |
| *Potentilla crantzii* | | 24 | P | | | | | | | 8 | ? |
| *Potentilla erecta* | - | 54 | P | VB | Sa | Jun 4 | S/CSR | | | x | 2 |
| *Primula farinosa* | | 45 | P | | | | | | | 9 | 2 |
| *Prunella vulgaris* | | 66 | P | (V) ?B | Ea | Jun 4 | CSR | 1.3 | -0.71 | 4 | x |
| *Pseudoscleropodium purum* | | 73 | | | | | | | | I | |
| *Ptilidium ciliare* | | 26 | | | | | | | | A | |
| *Racomitrium canescens* | - | 26 | | | | | | | | I | |
| *Racomitrium lanuginosum* | - | 26 | | | | | | | | I | |
| *Ranunculus acris* | | 35 | P | B V | Ea | May 3 | CSR | 10.7 | -0.71 | x | x |
| *Rhodobryum roseum* | | 56 | | | | | | | | I | |
| *Rhytidiadelphus loreus* | - | 52 | | | | | | | | I | |
| *Rhytidiadelphus squarrosus* | | 53 | | | | | | | | I | |
| *Rhytidiadelphus triquetrus* | | 56 | | | | | | | | I | |
| *Rhytidium rugosum* | | 26 | | | | | | | | | |
| *Rumex acetosa* | | 54 | P | S V | Ea | May 2 | CSR | 3.3 | 0.02 | x | 5 |

**Table (ii) continued**

| | Predominant change across the noda | Floristic element number | Longevity | Regenerative strategy | Leaf phenology | Flowering time and duration | C-S-R strategy | nDNA content | Standardised nDNA content | Reaction value | Nitrogen value |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Sanguisorba officinalis* | | 56 | P | | | | | | | x | 3 |
| *Scapania aspera* | - | 53 | | | | | | | | C | |
| *Selaginella selaginoides* | - | 46 | | | | | | | | 7 | 3 |
| *Sesleria albicans* | - | 53 | P | | | | | | | | |
| *Solorina saccata* | | | | | | | | | | C | |
| *Succisa pratensis* | | 74 | P | S | Ea | Jul 4 | S | 5.5 | 0.71 | x | 2 |
| *Taraxacum officinale* | | 66 | P | W | Ea | Mar 8 | R/CSR | 2.6 | -0.64 | x | 7 |
| *Thalictrum alpinum* | | 16 | P | | | | | | | | |
| *Thuidium delicatulum* | | 76 | | | | | | | | I | |
| *Thuidium philiberti* | | 76 | | | | | | | | C | |
| *Thuidium tamariscinum* | | 73 | | | | | | | | I | |
| *Thymus praecox* subsp. *arcticus* | - | 53 | P | V B | Ea | May 3 | S | 2.8 | 0.71 | 8 | 1 |
| *Tofieldia pusilla* | | 16 | P | | | | | | | | |
| *Tortella tortuosa* | - | 56 | | | | | | | | C | |
| *Trichostomium brachydontium* | | 92 | | | | | | | | I | |
| *Trifolium repens* | | 54 | P | (V) B | Ea | Jun 4 | CR/CSR | 3.1 | -0.52 | 7 | 1 |
| *Tritomaria quinquedentata* | | 26 | | | | | | | | A | |
| *Trollius europaeus* | | 43 | P | | | | | | | 7 | 6 |
| *Vaccinium myrtillus* | | 44 | P | V B | Sa | Apr 3 | SC | | | 2 | 3 |
| *Veronica officinalis* | | 53 | P | V B | | | S/CSR | | | 2 | 4 |
| *Vicia orobus* | | 72 | P | | | | | | | | |
| *Vicia sativa* | | 83 | A | | Sh | May 5 | | | | | |

## Table (ii) continued

| | Predominant change across the noda | Floristic element number | Longevity | Regenerative strategy | Leaf phenology | Flowering time and duration | C-S-R strategy | nDNA content | Standardised nDNA content | Reaction value | Nitrogen value |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Viola lutea* | + | 43 | P | | | | | | | | |
| *Viola riviniana* | | 73 | P | V S | Ea | Apr 3 | S | 2.7 | | | |
| *Viola riviniana* x *rupestris* | | 75 | P | | | | | | | | |
| *Viola rupestris* | - | 75 | P | | | | | | | 8 | 2 |

## Notes

1. Key to symbols: species increased/newly recorded (+), decreased/ now absent (-), ambiguous change (+/-) or no change (blank entry). See Section 4.2.2 for more details.
2. Floristic elements (listed completely in Table 2.1) are grouped into major biome categories: Arctic-montane (10), Boreo-arctic Montane (20), Wide-boreal (30), Boreal-montane (40), Boreo-temperate (50), Wide-temperate (60), Temperate (70), Southern-temperate (80) and Mediterannean (90).
3. Regenerative strategies: V= vegetative reproduction, S= seasonal regeneration where independent offspring, either seeds or propagules are produced in a single cohort, B= persistent seed or spore bank with viable but dormant seeds present throughout the year with some persisting over 12 months, W= production of widely dispersed seeds or spores,?=strategies of regeneration via seed production are uncertain.
4. Leaf phenology classes: First letter indicates whether canopy seasonal =S, or Evergreen =E. Sa= aestival i.e. canopy duration between spring and autumn, Sh= hibernal, autumn to early summer, Sv= vernal, winter to spring. Ea= always evergreen, Ep= partially evergreen i.e. whether evergreen depends on site growing at and severity of the winter. It may also mean that leaves partially senesce or that small shoots formed in autumn are those which overwinter.
5. Flowering time and duration: The month is the time of first flowering, followed by the number of months over which flowering will typically continue.
6. C-S-R strategy: C= competitor, S= stress-tolerator, R= ruderal. Intermediate strategies are also given e.g. SR is a stress-tolerant ruderal, S/SR is intermediate between a stress-tolerator and stress-tolerant ruderal.
7. Standardised nDNA content: See text, Section 4.1 for details of calculation and Table (i) in Appendix C.
8. Reaction value: See text, Section 4.1. The scale is reproduced earlier in this appendix.
9. Nitrogen value: See text, Section 4.1. The scale is reproduced earlier in this appendix.

# Appendix D

### Plant collection sites

For Nodum 4 collecting was carried out in the area around quadrat 110 (see vegetation map Sheet 3), for Nodum 21 in the area around quadrat 137 (also marked on Sheet 3) and for Nodum 33 the large patch by the reserve gate on the Sand Sike side G. R. NY815305 (See vegetation map Sheet 1).

### Setup of the microcosm frames

The frame was orientated north-west in all cases (this was the most efficient use of space at the smallest enclosure, on Widdybank Fell). The pots were arranged in the frame so they were c. 5 cm apart and 10 cm from the frame edge. The pots were buried up to their rims in sand and such that the plants they contained were at the same height as the top of the frame. Sand tended to blow away after a time so occasionally had to be replaced. The position of the "front" of each pot was marked using a plant label so that after monitoring the pot could be replaced in the frame in the same position.

**Table (i) Results from Mann-Whitney U-tests comparing Domin data between the survey of Willis (1995) and Jones (1973) for three vegetation noda. U values and significance levels (*where P≤0.05, **where P≤0.01) are given. Species are given frequency values (F) and median score on the Domin scale (D) for both surveys. Changes in species frequency or abundance between surveys are indicated as species unchanged (u) now increased (+) decreased (-) new (N) or changing differently in frequency and abundance, respectively (+/- ). Refer to text for more detailed explanation of these symbols.**

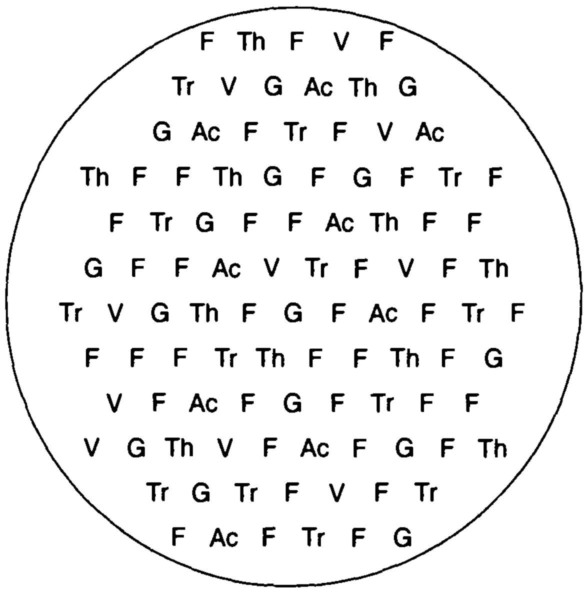
| | NODUM 4 | | | | | | NODUM 21 | | | | | | NODUM 33 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Jones | | Willis | | Mann-Whitney test | | Jones | | Willis | | Mann-Whitney test | | Jones | | Willis | | Mann-Whitney test | |
| Number of quadrats | 12 | | 18 | | | | 8 | | 19 | | | | 7 | | 16 | | | |
| Total number of species recorded | 96 | | 82 | | | | 101 | | 98 | | | | 59 | | 72 | | | |
| Critical values for U with number of quadrats as above | p≤0.05 =155<br>p≤0.01 =169 | | | | | | p≤0.05 =114<br>p≤0.01 =124 | | | | | | p≤0.05 =86<br>p≤0.01 =94 | | | | | |
| | F | D | F | D | value of U | change | F | D | F | D | value of U | change | F | D | F | D | value of U | change |
| *Achillea millefolium* | | | | | | | 0.72 | 2 | 0.74 | 2 | 93.5 | u | | | 0.69 | 3 | 94.5** | N |
| *Agrostis vinealis* | | | 0.28 | 2 | 138.0 | N | | | | | | | | | | | | |
| *Festuca ovina* | | | | | | | 1.00 | 6.5 | 0.95 | 7.5 | 118.0* | + | 1 | 6 | 1 | 8 | 91.0* | + |
| *Galium saxatile* | | | | | | | | | | | | | 0.86 | 5 | 0.81 | 3 | 89.5* | - |
| *Thymus praecox* subsp. *arcticus* | | | | | | | 1 | 5.5 | 1 | 3 | 139.5** | - | | | 0.75 | 3 | 98.0** | N |
| *Sesleria albicans* | 1 | 4.5 | 0.94 | 4 | 114.5 | - | | | | | | | | | | | | |
| *Trifolium repens* | | | | | | | 1.00 | 4 | 0.84 | 2 | 119.0* | - | 0.29 | 3.5 | 0.81 | 4 | 84.0 | + |
| *Viola lutea* | | | | | | | 1.00 | 2.5 | 0.79 | 2 | 112.5 | - | 0.14 | 4 | 0.88 | 2 | 90.0* | +/- |

**Table (ii) Grits used in the microcosms.**

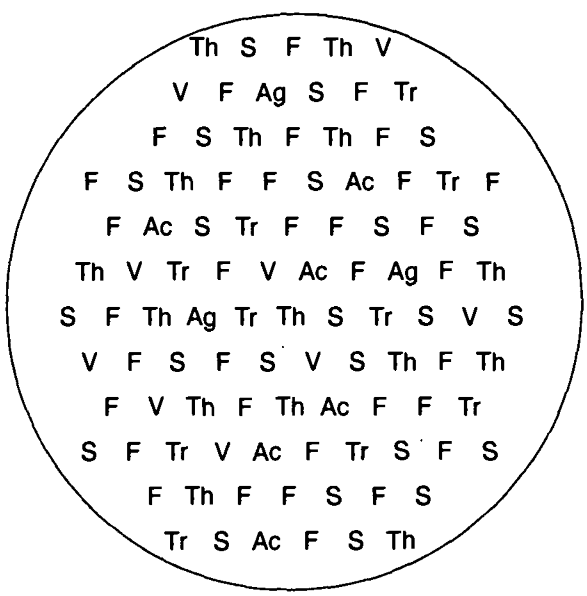
| Grit | Type or brand | Source | Median pH of washed grit (n=4) | Range (n=4) |
|---|---|---|---|---|
| coarse chippings | | local garden centre | 6.5 | 0.75 |
| "Lytag" | | local garden centre | 6.5 | 0.23 |
| coarse quartzite grit lime-free horticultural grade | William Sinclair Horticulture Limited, Lincoln | local garden centre | 6.8 | 0.08 |
| limestone chippings | Oxford Limestone | Barrasford quarry, Northumberland G. R. NY914745 | 7.6 | 0.08 |
| flint grit | "Jondo" flint hen grit | agricultural supplier | 6.5 | 0.13 |

**Figure (i) The planting design adopted for the Nodum 33 and Nodum 21 & 4 microcosms.**

**Nodum 33 microcosms**



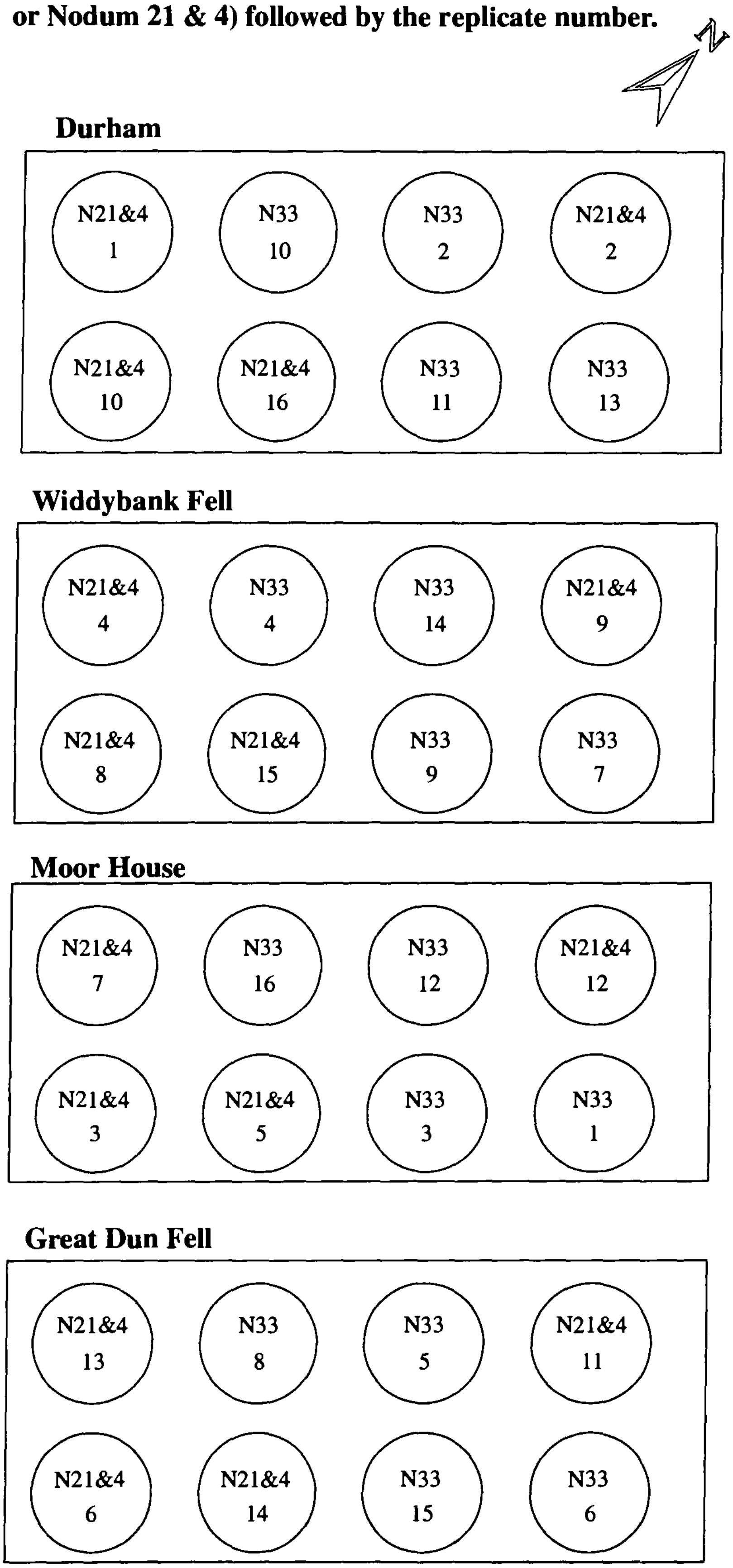

**Nodum 21 & 4 microcosms**

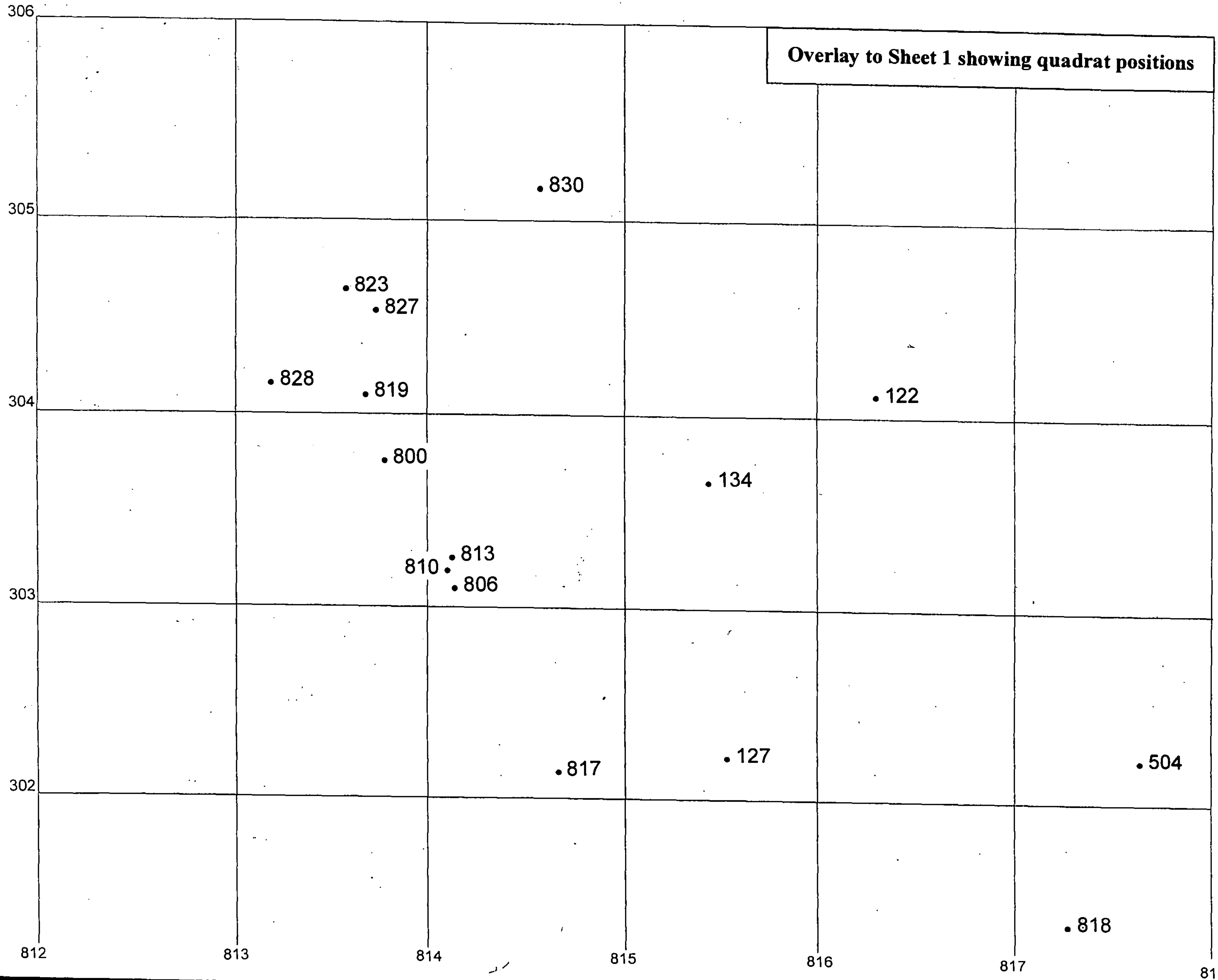


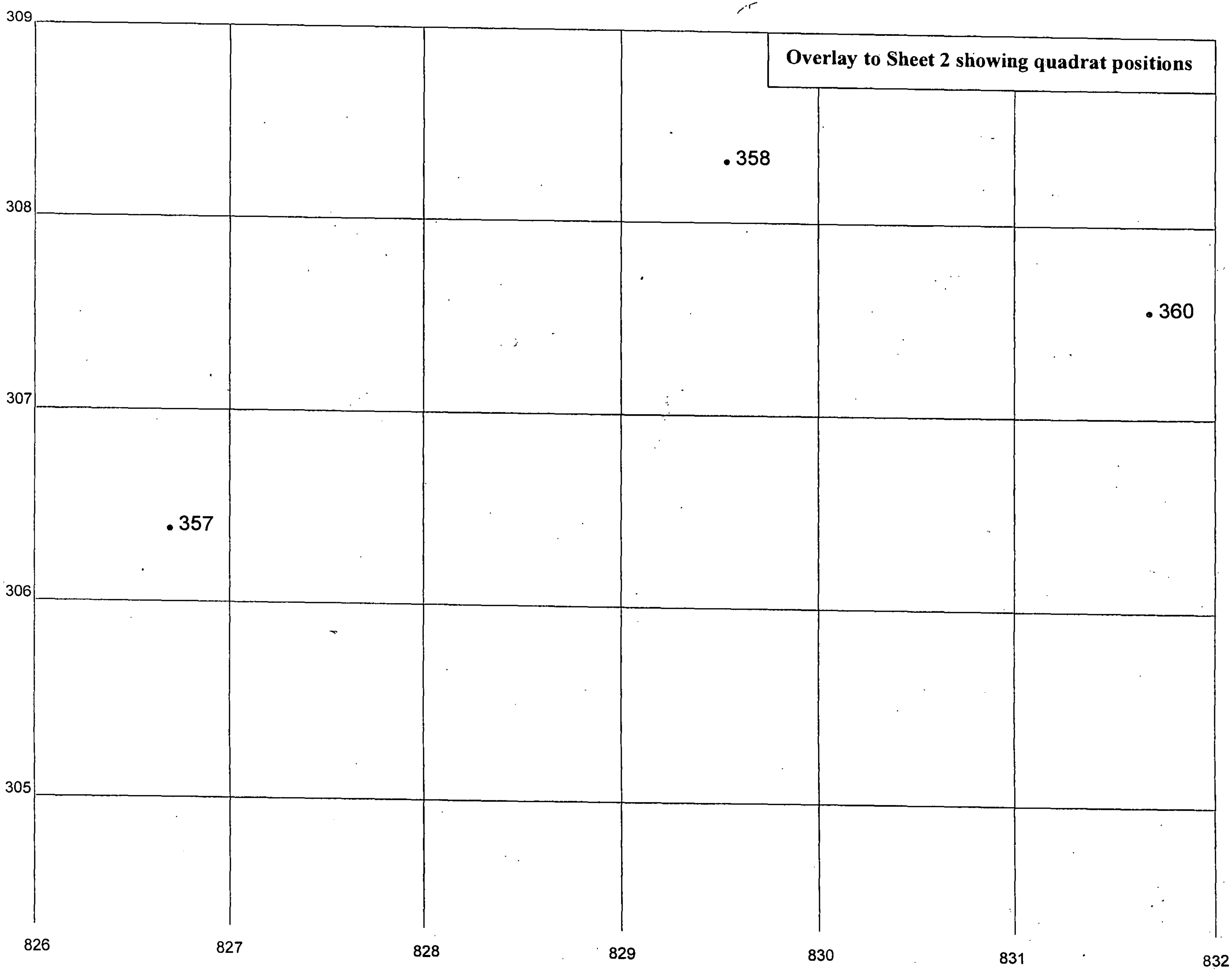

Key to species used in both microcosm types

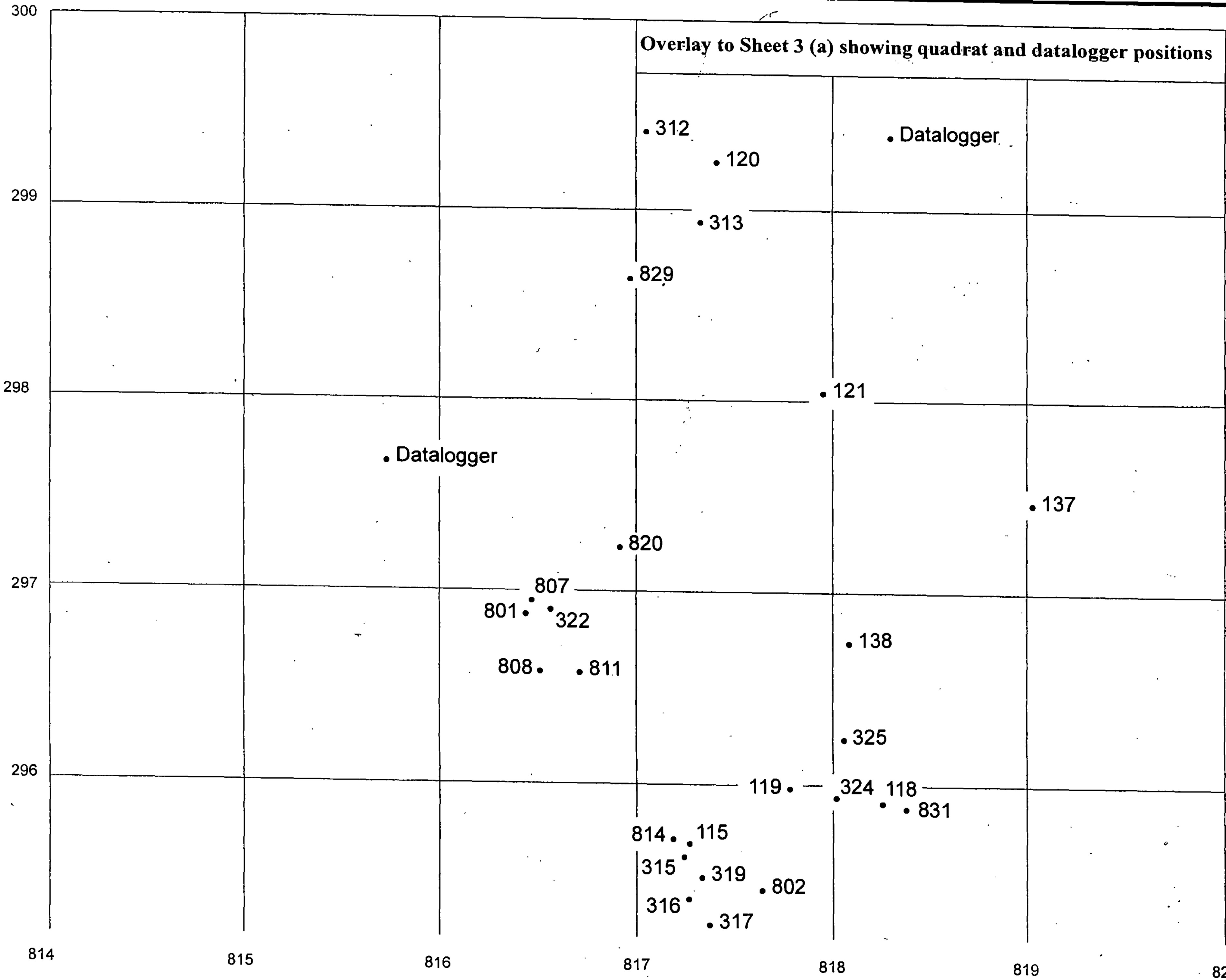
- Ac *Achillea millefolium*
- Ag *Agrostis vinealis*
- F *Festuca ovina*
- S *Sesleria albicans*
- Th *Thymus praecox* subsp. *arcticus*
- Tr *Trifolium repens*
- V *Viola lutea*
- G *Galium saxatile*

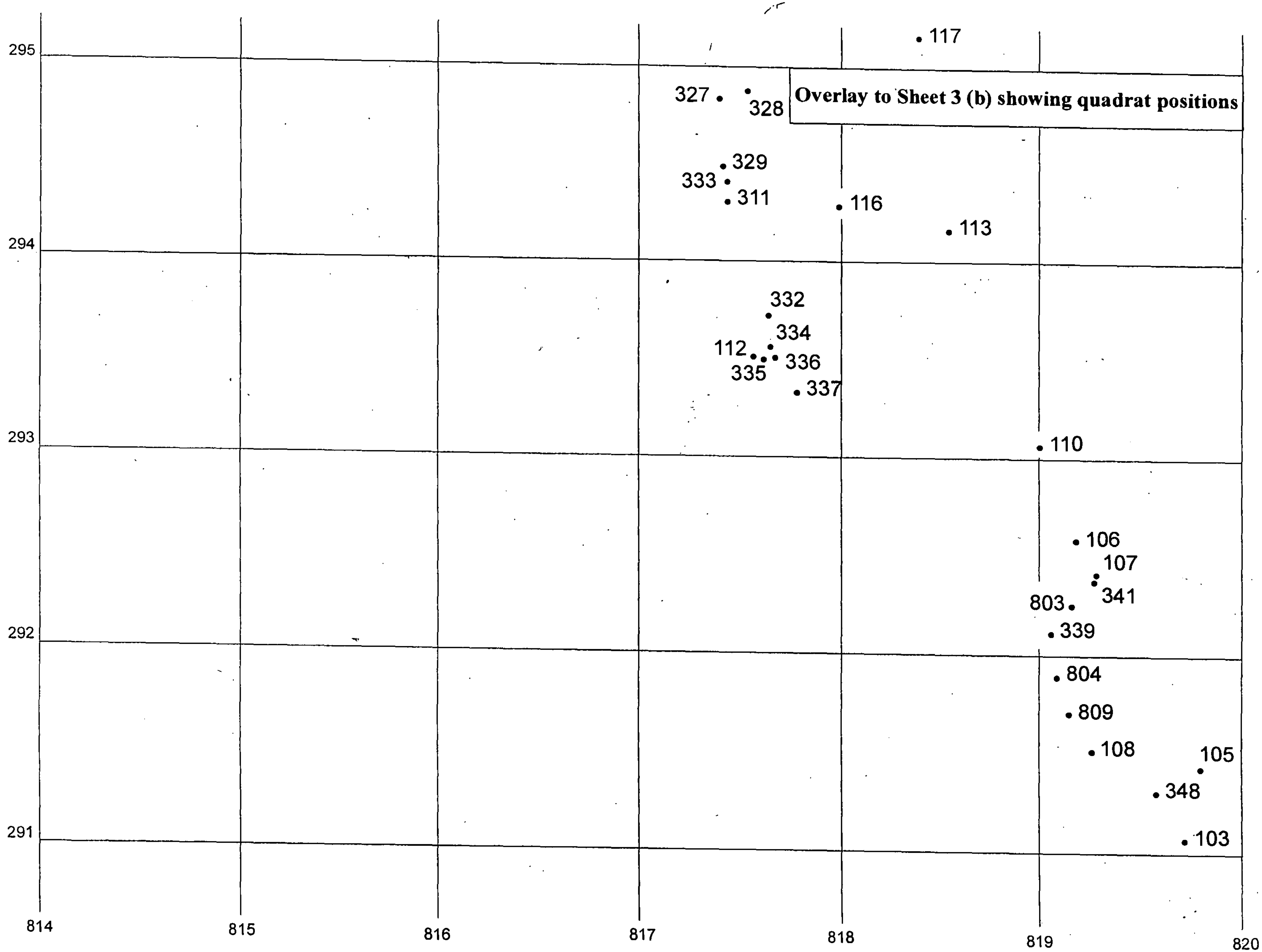
**Figure (ii) Arrangement of replicate microcosms in the frames at the four sites along the altitudinal gradient. The microcosm type is given (Nodum 33 or Nodum 21 & 4) followed by the replicate number.**



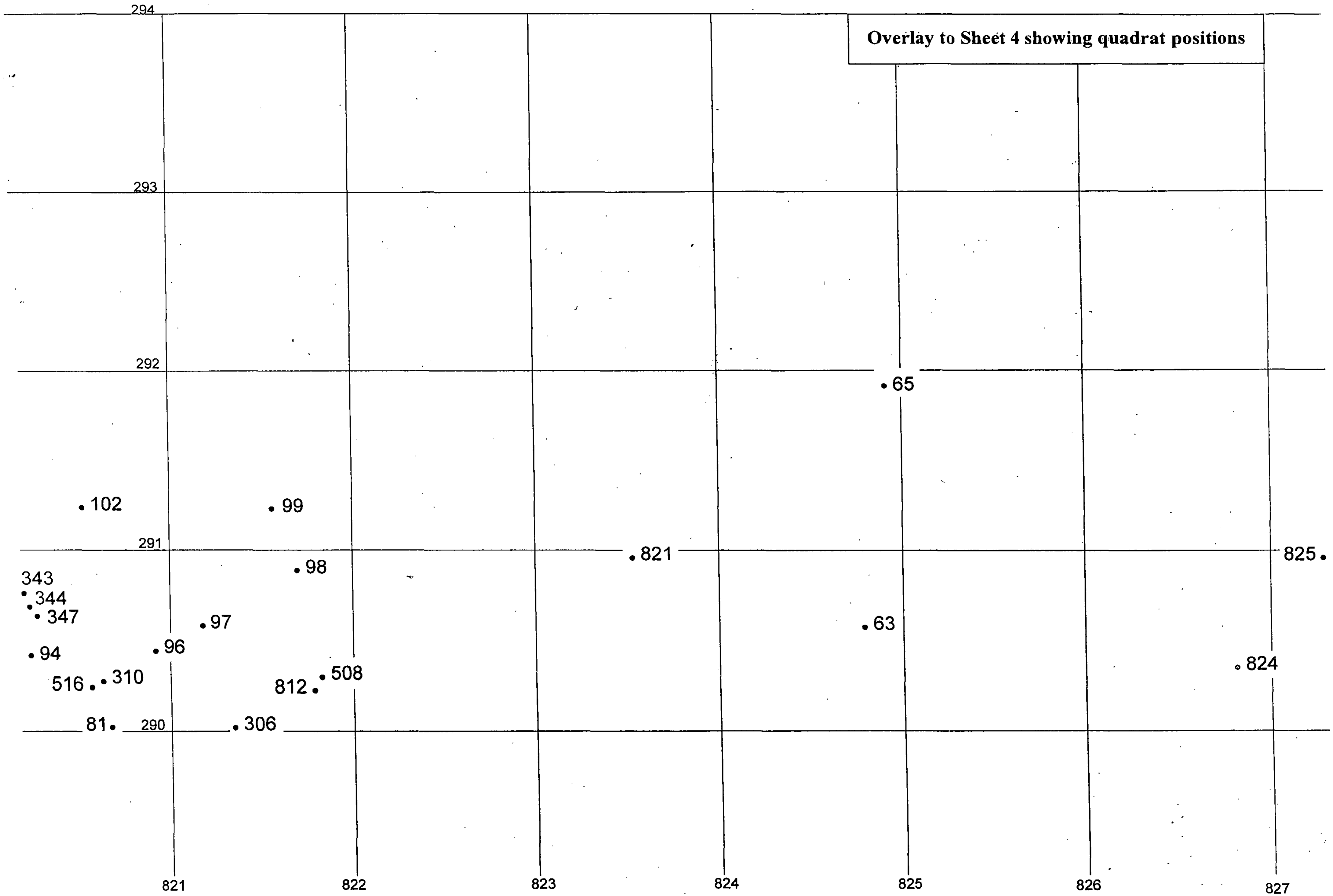

Overlay to Sheet 1 showing quadrat positions
306
305
304
303
302
812
813
814
815
816
817
818
830
823
827
828
819
122
800
134
813
810
806
817
127
504
818


Overlay to Sheet 2 showing quadrat positions
309
308
307
306
305
826
827
828
829
830
831
832
358
360
357

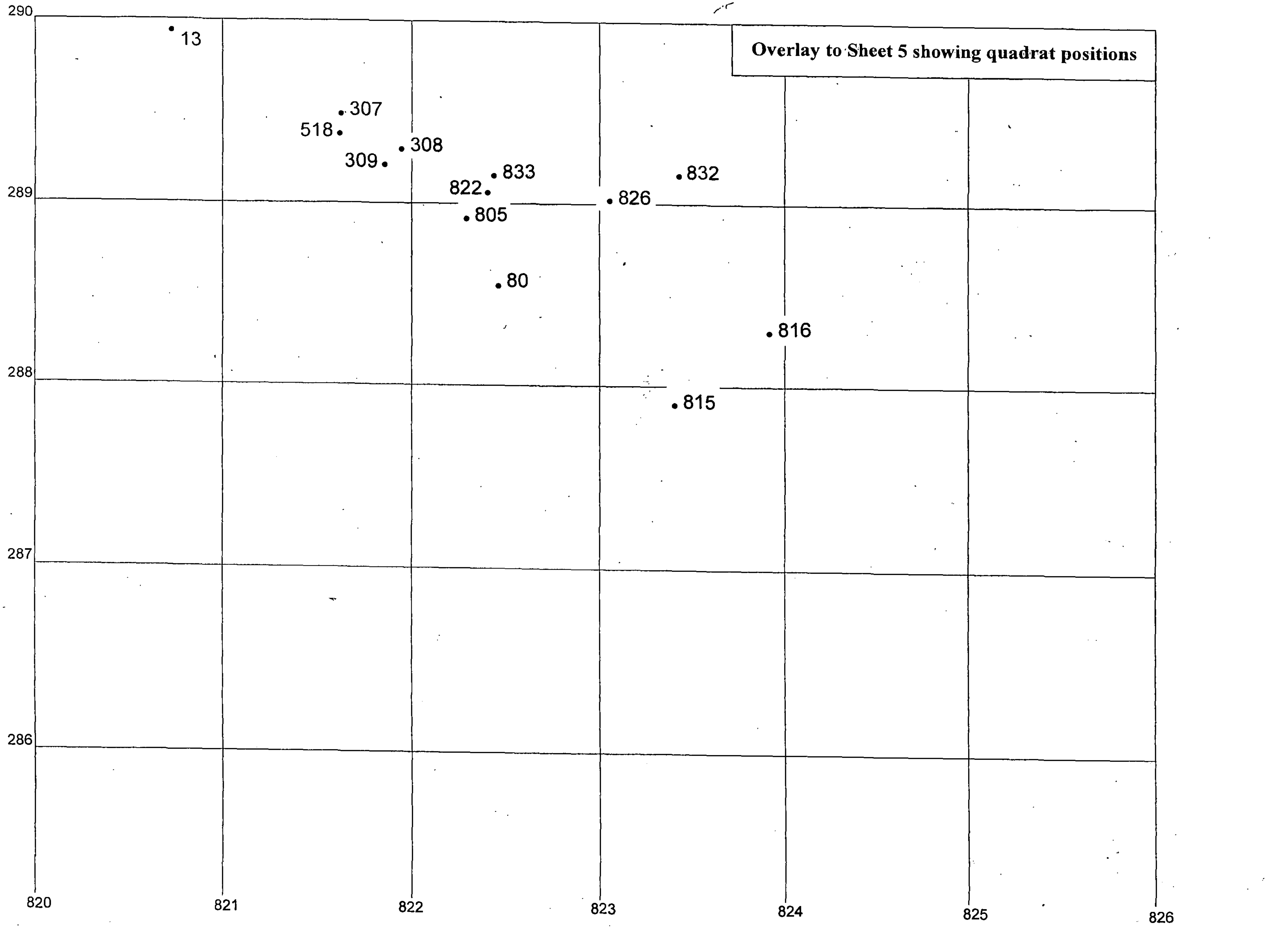

Overlay to Sheet 3 (a) showing quadrat and datalogger positions
300
299
298
297
296
814
815
816
817
818
819
820
312
120
Datalogger
313
829
121
Datalogger
137
820
807
801
322
138
808
811
325
119
324
118
831
814
115
315
319
802
316
317



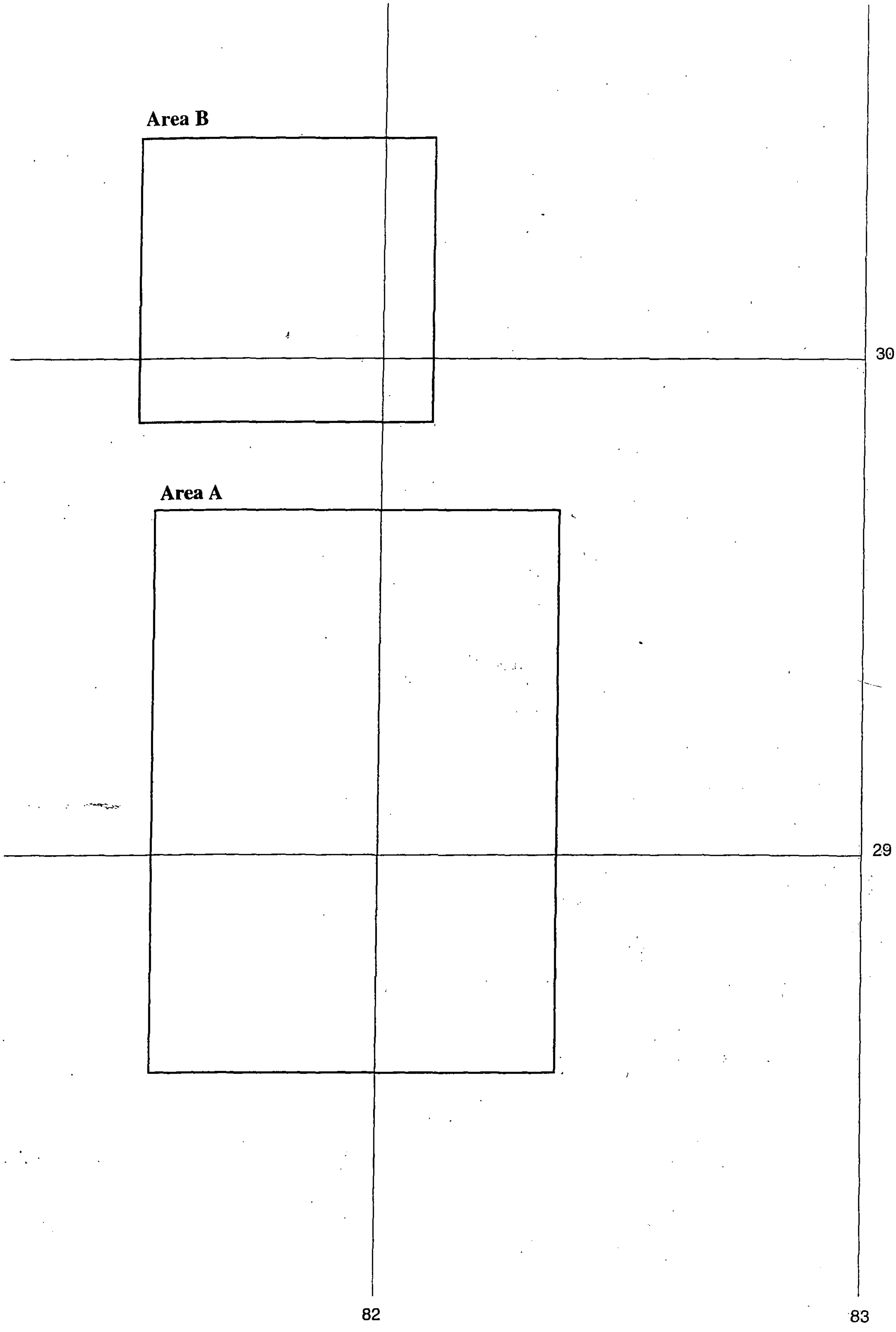
Overlay to Sheet 3 (b) showing quadrat positions



Overlay to Sheet 4 showing quadrat positions
294
293
292
291
290
821
822
823
824
825
826
827
65
102
99
821
825
98
343
344
347
97
63
96
94
824
310
508
516
812
81
306


Overlay to Sheet 5 showing quadrat positions
290
289
288
287
286
820
821
822
823
824
825
826
13
307
518
308
309
833
832
822
826
805
80
816
815

**Overlay for 1:10000 vegetation map to show areas covered by aerial photos, Plates 3.1-3.4.**



1:2500

# WIDDYBANK FELL

## RED SIKE

Vegetation SHEET 3




250 0 feet 250 500 750

100 50 0 metres 100 200

SCALE 1:2500

Heights in metres above Ordnance Datum.

Contour interval 2 metres.

Aerial photography dated Oct. 1969 by Meridian Airmaps Ltd., Lancing, Sussex.

Field survey for control of photogrammetric mapping by Department of Surveying, University of Newcastle upon Tyne.

Vegetation survey prepared from ground observations and air photograph interpretation by A. V. Jones, B.Sc., University of Durham.

Photogrammetric mapping and fair drawing by M. S. Evans, Department of Surveying, University of Newcastle upon Tyne.

Additional cartographic work and printing by A. W. Gatrell & Co. Ltd., London.

## VEGETATION CLASSIFICATION

| | |
|---|---|
| 1–7 | Class: Festuco-Brometea (calcareous lowland grasslands)<br>Order: Brometalia erecti (dry and semi-dry grasslands)<br>Alliance: Mesobromion erecti<br>Sub Alliance: Seslerio-Mesobromion (short grassland) |
| V | Class: Violetea calaminariae (vegetation on soils rich in heavy metals)<br>Order: Violetalia calaminariae<br>Alliance: Thlaspion calaminariae (pioneer communities of the class) |
| ▲ | Class: Montio-Cardaminetea (vegetation of spring-heads)<br>Order: Montio-Cardaminetalia<br>Alliance: Cratoneurion commutati (vegetation of tufaceous springs) |
| 19–22 | Class: Molinio-Arrhenatheretea (cultivated rich pastures and marshy meadows)<br>Order: Arrhenatheretalia (species-rich meadows and pastures)<br>Alliance: Ranunculo-Anthoxanthion (sub-alpine meadows and pastures) |
| 15–18 | Class: Parvocaricetea (short-sedge marsh)<br>Order: Caricetalia nigrae (mesotrophic sedge marsh)<br>Alliance: Caricion curto-nigrae |
| 8–14 | Order: Tofieldietalia (calcareous sedge marsh)<br>Alliance: Caricion davallianae |
| 23 | Class: Oxycocco-Sphagnetea (bogs and wet heaths)<br>Order: Ericetalia tetralicis (wet heaths)<br>Alliance: Ericion tetralicis |
| 24, 28 | Order: Sphagnetalia magellanici (ombrogenous bogs)<br>Alliance: Erico-Sphagnion |
| 25, 27, 29 | Class: Nardo-Callunetea (grass heath)<br>Order: Nardetalia (acid grassland)<br>Alliance: Violion caninae |
| 26<br>31, 32, 33 | Order: Calluno-Ulicetalia (heath)<br>Alliance: Empetrion boreale |
| I–X | Vegetation of uncertain phytosociological affinities and fragmentary units.<br>(For details see booklet) |
| 25/9 | Complex of hummock-hollow vegetation: 25 forming hummocks, 9 forming hollows. |
| V 21 | Complex of two Alliances along line of old mineral vein: V along sides of channel, 21 on base. |
| 5, 33 | Complex of two Alliances: mosaic of units as indicated. |
| | Areas without vegetation—natural or man-made |

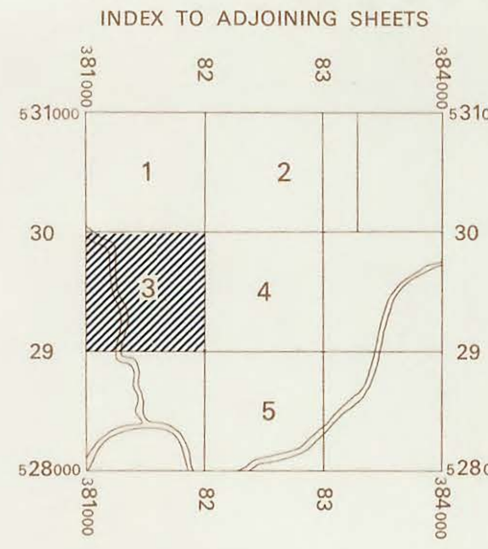
## LEGEND

| | |
|---|---|
| river, stream, sike | |
| surface water | W |
| fence, wall | |
| road, track (fenced and unfenced) | |
| building | |
| contours (metres) | 500 |
| spot level (metres) | . 525·6 |

This sheet is one of a series of five maps at 1:2500 scale which cover Widdybank Fell, part of the Upper Teesdale Nature Reserve.

The maps are the result of a research project financed by the Teesdale Trust and carried out in the Universities of Durham and Newcastle upon Tyne under the supervision of M. E. Bradshaw, Ph.D. and I. Newton, M.Sc.

INDEX TO ADJOINING SHEETS



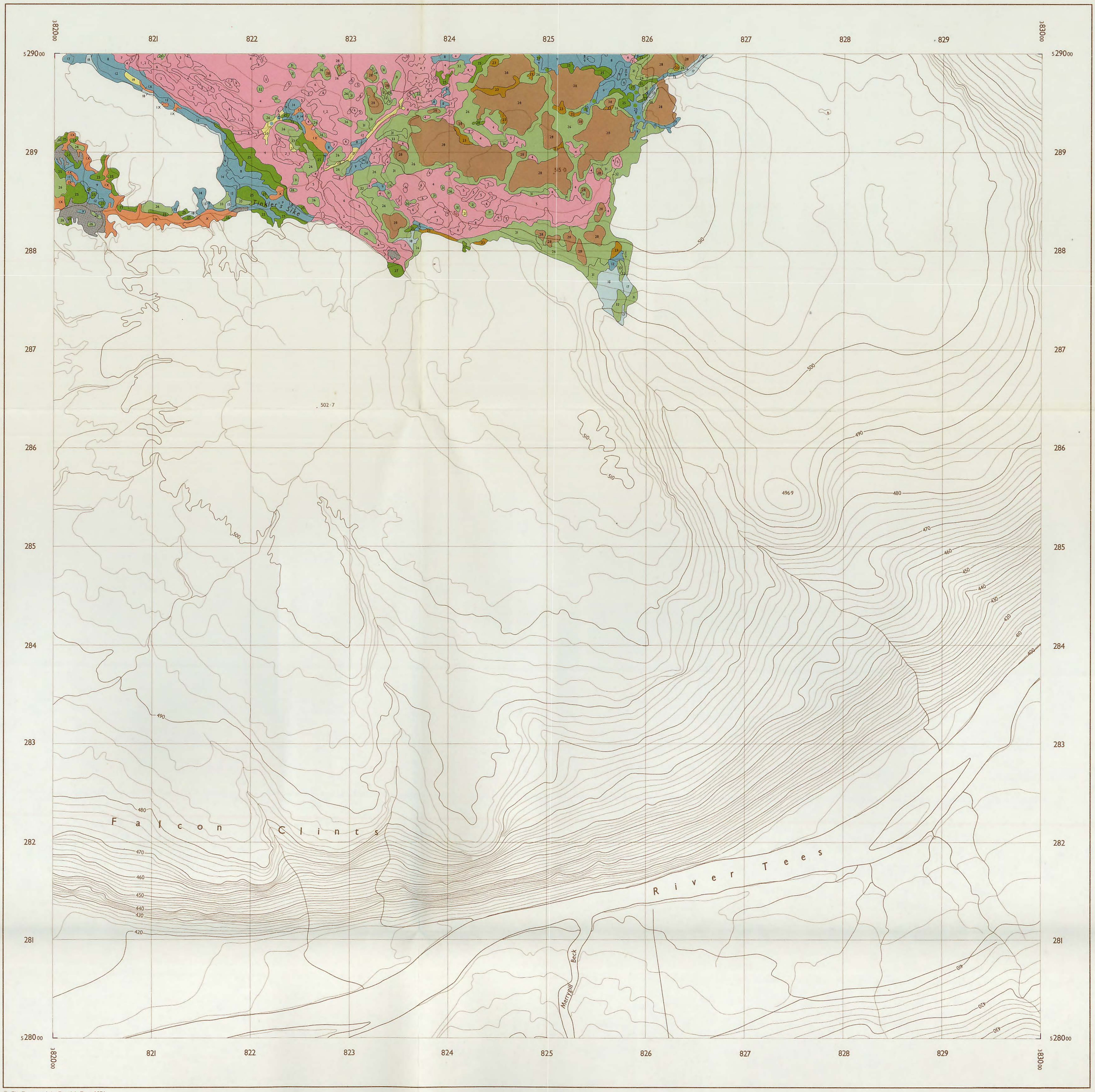

Additional maps, together with a descriptive booklet by M. E. Bradshaw, Ph.D. and A. V. Jones, B.Sc., outlining the classificatory system used, are available from:–The Secretary,
Department of Extra-Mural Studies,
University of Durham,
32 Old Elvet,
Durham.

# WIDDYBANK FELL

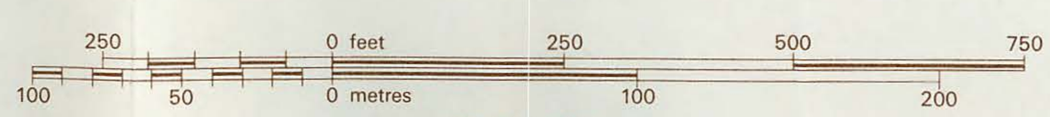
## TINKLER'S SIKE

1:2500

Vegetation SHEET 5






SCALE 1:2500
Heights in metres above Ordnance Datum.
Contour interval 2 metres.

## VEGETATION CLASSIFICATION

- 1–7 — Class: Festuco-Brometea (calcareous lowland grasslands)
  Order: Brometalia erecti (dry and semi-dry grasslands)
  Alliance: Mesobromion erecti
  Sub Alliance: Seslerio-Mesobromion (short grassland)
- V — Class: Violetea calaminariae (vegetation on soils rich in heavy metals)
  Order: Violetalia calaminariae
  Alliance: Thlaspion calaminariae (pioneer communities of the class)
- ▲ — Class: Montio-Cardaminetea (vegetation of spring-heads)
  Order: Montio-Cardaminetalia
  Alliance: Cratoneurion commutati (vegetation of tufaceous springs)
- 19–22 — Class: Molinio-Arrhenatheretea (cultivated rich pastures and marshy meadows)
  Order: Arrhenatheretalia (species-rich meadows and pastures)
  Alliance: Ranunculo-Anthoxanthion (sub-alpine meadows and pastures)
- 15–18 — Class: Parvocaricetea (short-sedge marsh)
  Order: Caricetalia nigrae (mesotrophic sedge marsh)
  Alliance: Caricion curto-nigrae
- 8–14 — Order: Tofieldietalia (calcareous sedge marsh)
  Alliance: Caricion davallianae
- 23 — Class: Oxycocco-Sphagnetea (bogs and wet heaths)
  Order: Ericetalia tetralicis (wet heaths)
  Alliance: Ericion tetralicis
- 24, 28 — Order: Sphagnetalia magellanici (ombrogenous bogs)
  Alliance: Erico-Sphagnion
- 25, 27, 29 — Class: Nardo-Callunetea (grass heath)
  Order: Nardetalia (acid grassland)
  Alliance: Violion caninae
- 26, 31, 32, 33 — Order: Calluno-Ulicetalia (heath)
  Alliance: Empetrion boreale
- 1–X — Vegetation of uncertain phytosociological affinities and fragmentary units. (For details see booklet)
- 25/9 — Complex of hummock-hollow vegetation: 25 forming hummocks, 9 forming hollows.
- V 21 — Complex of two Alliances along line of old mineral vein: V along sides of channel, 21 on base.
- 5, 33 — Complex of two Alliances: mosaic of units as indicated.
- Areas without vegetation—natural or man-made

Aerial photography dated Oct. 1969 by Meridian Airmaps Ltd., Lancing, Sussex.

Field survey for control of photogrammetric mapping by Department of Surveying, University of Newcastle upon Tyne.

Vegetation survey prepared from ground observations and air photograph interpretation by A. V. Jones, B.Sc., University of Durham.

Photogrammetric mapping and fair drawing by M. S. Evans. Department of Surveying, University of Newcastle upon Tyne.

Additional cartographic work and printing by A. W. Gatrell & Co. Ltd., London.

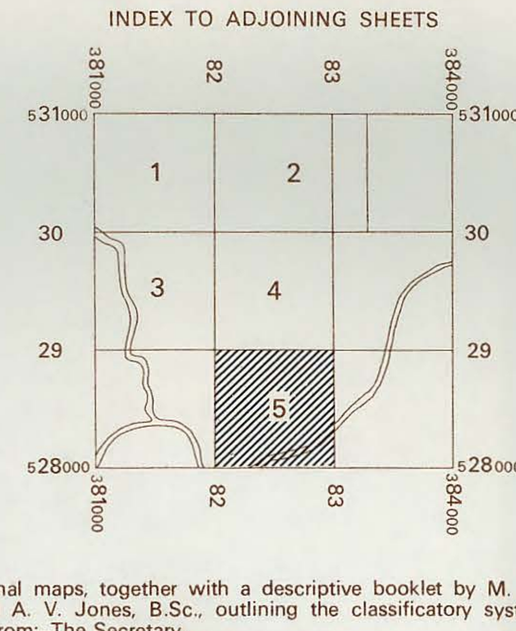
### LEGEND

- river, stream, sike
- surface water
- fence, wall
- road, track (fenced and unfenced)
- building
- contours (metres)
- spot level (metres) — .525·6

This sheet is one of a series of five maps at 1:2500 scale which cover Widdybank Fell, part of the Upper Teesdale Nature Reserve.

The maps are the result of a research project financed by the Teesdale Trust and carried out in the Universities of Durham and Newcastle upon Tyne under the supervision of M. E. Bradshaw, Ph.D. and I. Newton, M.Sc.

### INDEX TO ADJOINING SHEETS



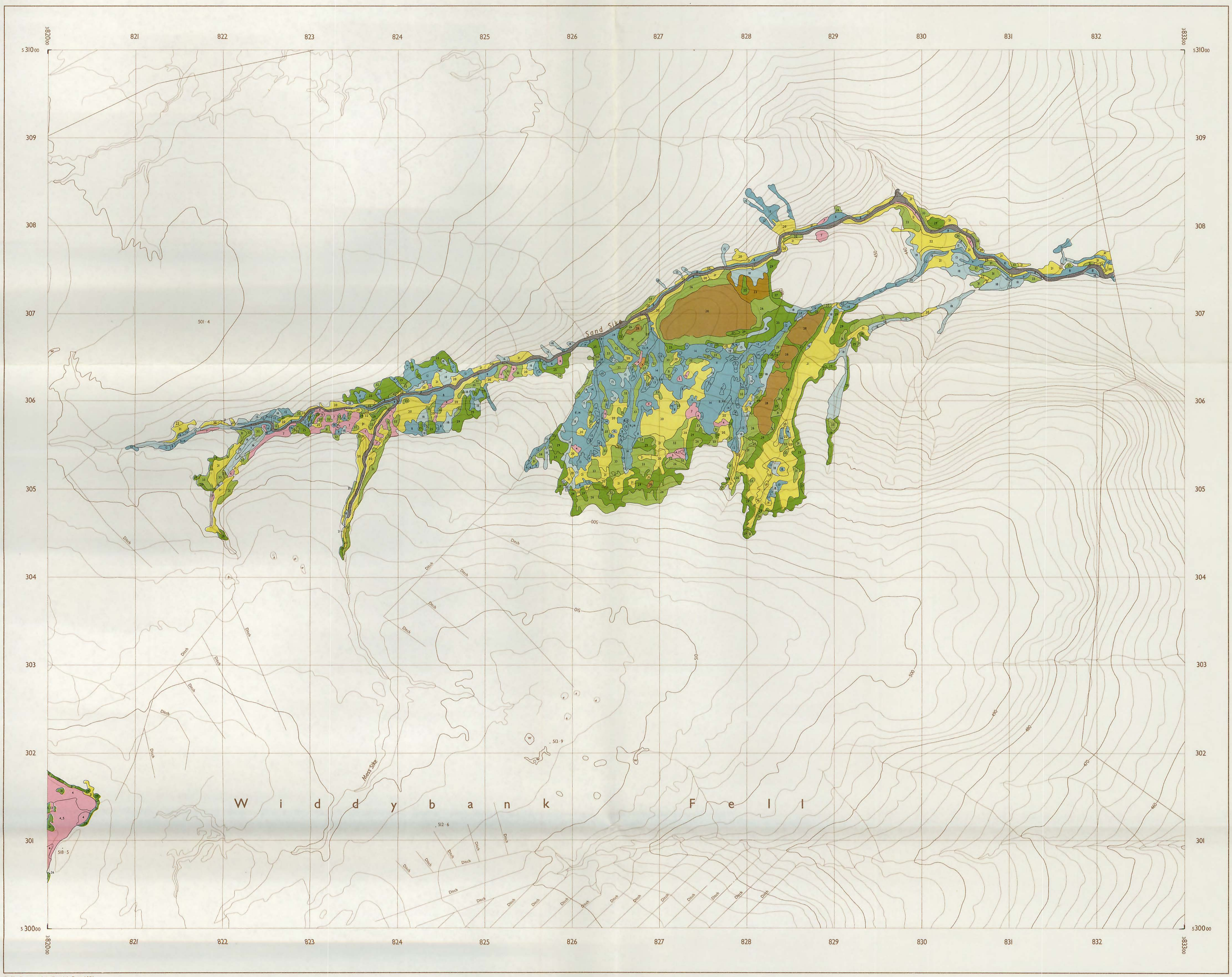

Additional maps, together with a descriptive booklet by M. E. Bradshaw, Ph.D. and A. V. Jones, B.Sc., outlining the classificatory system used, are available from:—The Secretary,
Department of Extra-Mural Studies,
University of Durham,
32 Old Elvet,
Durham.

# WIDDYBANK FELL

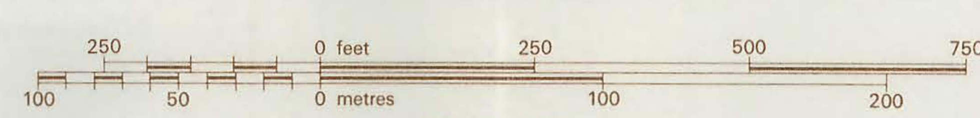
## SAND SIKE

1:2500

Vegetation SHEET 2






SCALE 1:2500

Heights in metres above Ordnance Datum.

Contour interval 2 metres.


Aerial photography dated Oct. 1969 by Meridian Airmaps Ltd., Lancing, Sussex.

Field survey for control of photogrammetric mapping by Department of Surveying, University of Newcastle upon Tyne.

Vegetation survey prepared from ground observations and air photograph interpretation by A. V. Jones, B.Sc., University of Durham.

Photogrammetric mapping and fair drawing by M. S. Evans, Department of Surveying, University of Newcastle upon Tyne.

Additional cartographic work and printing by A. W. Gatrell & Co. Ltd., London.


## LEGEND

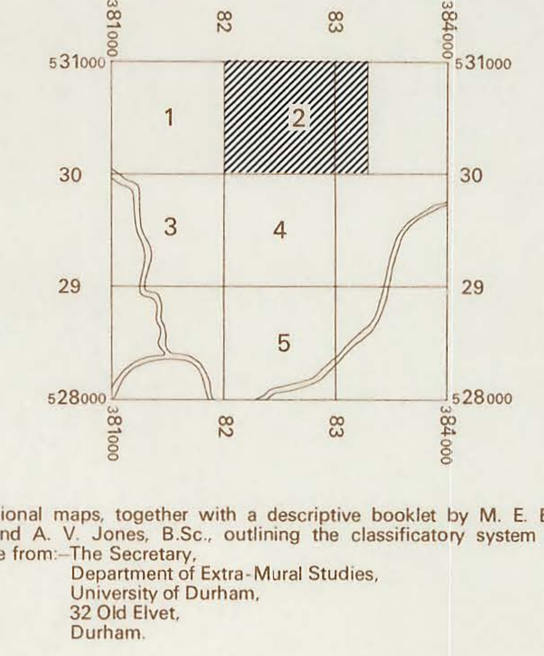
| | |
|---|---|
| river, stream, sike | |
| surface water | W |
| fence, wall | |
| road, track (fenced and unfenced) | |
| building | |
| contours (metres) | 500 |
| spot level (metres) | . 525·6 |

## VEGETATION CLASSIFICATION

| | |
|---|---|
| 1–7 | Class: Festuco-Brometea (calcareous lowland grasslands)<br>Order: Brometalia erecti (dry and semi-dry grasslands)<br>Alliance: Mesobromion erecti<br>Sub Alliance: Seslerio-Mesobromion (short grassland) |
| V | Class: Violetea calaminariae (vegetation on soils rich in heavy metals)<br>Order: Violetalia calaminariae<br>Alliance: Thlaspion calaminariae (pioneer communities of the class) |
| ▲ | Class: Montio-Cardaminetea (vegetation of spring-heads)<br>Order: Montio-Cardaminetalia<br>Alliance: Cratoneurion commutati (vegetation of tufaceous springs) |
| 19–22 | Class: Molinio-Arrhenatheretea (cultivated rich pastures and marshy meadows)<br>Order: Arrhenatheretalia (species-rich meadows and pastures)<br>Alliance: Ranunculo-Anthoxanthion (sub-alpine meadows and pastures) |
| 15–18 | Class: Parvocaricetea (short-sedge marsh)<br>Order: Caricetalia nigrae (mesotrophic sedge marsh)<br>Alliance: Caricion curto-nigrae |
| 8–14 | Order: Tofieldietalia (calcareous sedge marsh)<br>Alliance: Caricion davallianae |
| 23 | Class: Oxycocco-Sphagnetea (bogs and wet heaths)<br>Order: Ericetalia tetralicis (wet heaths)<br>Alliance: Ericion tetralicis |
| 24, 28 | Order: Sphagnetalia magellanici (ombrogenous bogs)<br>Alliance: Erico-Sphagnion |
| 25, 27, 29 | Class: Nardo-Callunetea (grass heath)<br>Order: Nardetalia (acid grassland)<br>Alliance: Violion caninae |
| 26<br>31, 32, 33 | Order: Calluno-Ulicetalia (heath)<br>Alliance: Empetrion boreale |
| 1–X | Vegetation of uncertain phytosociological affinities and fragmentary units.<br>(For details see booklet) |
| 25/9 | Complex of hummock-hollow vegetation: 25 forming hummocks, 9 forming hollows. |
| V 21 | Complex of two Alliances along line of old mineral vein: V along sides of channel, 21 on base. |
| 5, 33 | Complex of two Alliances: mosaic of units as indicated. |
| | Areas without vegetation—natural or man-made |


This sheet is one of a series of five maps at 1:2500 scale which cover Widdybank Fell, part of the Upper Teesdale Nature Reserve.
The maps are the result of a research project financed by the Teesdale Trust and carried out in the Universities of Durham and Newcastle upon Tyne under the supervision of M. E. Bradshaw, Ph.D and I. Newton, M.Sc.


### INDEX TO ADJOINING SHEETS



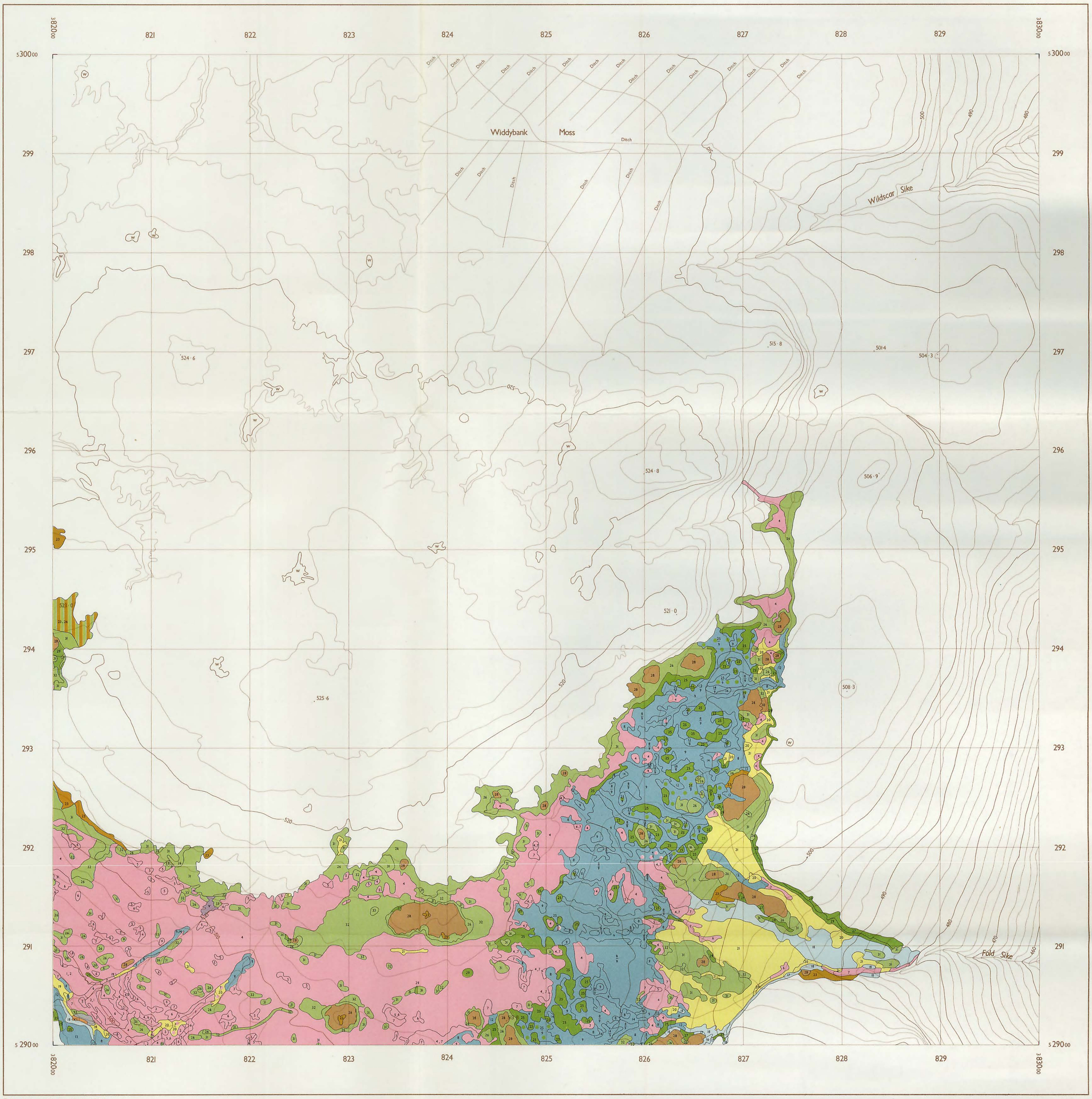

Additional maps, together with a descriptive booklet by M. E. Bradshaw, Ph.D. and A. V. Jones, B.Sc., outlining the classificatory system used, are available from:–The Secretary,
Department of Extra-Mural Studies,
University of Durham,
32 Old Elvet,
Durham.

# WIDDYBANK FELL

## FOLD SIKE

1:2500

Vegetation SHEET 4






250 0 feet 250 500 750

100 50 0 metres 100 200

SCALE 1:2500

Heights in metres above Ordnance Datum.

Contour interval 2 metres.

## VEGETATION CLASSIFICATION

1–7 — Class: Festuco-Brometea (calcareous lowland grasslands)
Order: Brometalia erecti (dry and semi-dry grasslands)
Alliance: Mesobromion erecti
Sub Alliance: Seslerio-Mesobromion (short grassland)

V — Class: Violetea calaminariae (vegetation on soils rich in heavy metals)
Order: Violetalia calaminariae
Alliance: Thlaspion calaminariae (pioneer communities of the class)

▲ — Class: Montio-Cardaminetea (vegetation of spring-heads)
Order: Montio-Cardaminetalia
Alliance: Cratoneurion commutati (vegetation of tufaceous springs)

19–22 — Class: Molinio-Arrhenatheretea (cultivated rich pastures and marshy meadows)
Order: Arrhenatheretalia (species-rich meadows and pastures)
Alliance: Ranunculo-Anthoxanthion (sub-alpine meadows and pastures)

15–18 — Class: Parvocaricetea (short-sedge marsh)
Order: Caricetalia nigrae (mesotrophic sedge marsh)
Alliance: Caricion curto-nigrae

8–14 — Order: Tofieldietalia (calcareous sedge marsh)
Alliance: Caricion davallianae

23 — Class: Oxycocco-Sphagnetea (bogs and wet heaths)
Order: Ericetalia tetralicis (wet heaths)
Alliance: Ericion tetralicis

24,28 — Order: Sphagnetalia magellanici (ombrogenous bogs)
Alliance: Erico-Sphagnion

25,27,29 — Class: Nardo-Callunetea (grass heath)
Order: Nardetalia (acid grassland)
Alliance: Violion caninae

26, 31,32,33 — Order: Calluno-Ulicetalia (heath)
Alliance: Empetrion boreale

1–X — Vegetation of uncertain phytosociological affinities and fragmentary units.
(For details see booklet)

25/9 — Complex of hummock-hollow vegetation: 25 forming hummocks, 9 forming hollows.

V 21 — Complex of two Alliances along line of old mineral vein: V along sides of channel, 21 on base.

5, 33 — Complex of two Alliances: mosaic of units as indicated.

Areas without vegetation—natural or man-made

Aerial photography dated Oct. 1969 by Meridian Airmaps Ltd., Lancing, Sussex.

Field survey for control of photogrammetric mapping by Department of Surveying, University of Newcastle upon Tyne.

Vegetation survey prepared from ground observations and air photograph interpretation by A. V. Jones, B.Sc., University of Durham.

Photogrammetric mapping and fair drawing by M. S. Evans, Department of Surveying, University of Newcastle upon Tyne.

Additional cartographic work and printing by A. W. Gatrell & Co. Ltd., London.

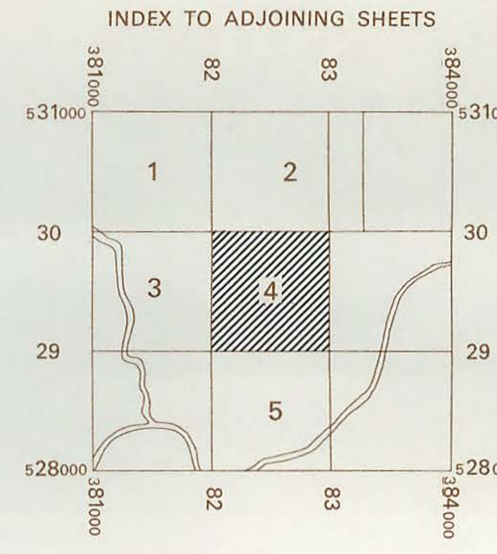
## LEGEND

| | |
|---|---|
| river, stream, sike | |
| surface water | W |
| fence, wall | |
| road, track (fenced and unfenced) | |
| building | |
| contours (metres) | 500 |
| spot level (metres) | . 525·6 |

This sheet is one of a series of five maps at 1:2500 scale which cover Widdybank Fell, part of the Upper Teesdale Nature Reserve.

The maps are the result of a research project financed by the Teesdale Trust and carried out in the Universities of Durham and Newcastle upon Tyne under the supervision of M. E. Bradshaw, Ph.D. and I. Newton, M.Sc.

INDEX TO ADJOINING SHEETS




Additional maps, together with a descriptive booklet by M. E. Bradshaw, Ph.D. and A. V. Jones, B.Sc., outlining the classificatory system used, are available from:–The Secretary,
Department of Extra-Mural Studies,
University of Durham,
32 Old Elvet,
Durham.

# WIDDYBANK FELL

## SLAPESTONE SIKE

1:2500

Vegetation SHEET 1




| 250 | | 0 feet | 250 | 500 | 750 |
|---|---|---|---|---|---|
| 100 | 50 | 0 metres | 100 | 200 | |

SCALE 1:2500

Heights in metres above Ordnance Datum.

Contour interval 2 metres.

## VEGETATION CLASSIFICATION

| Units | Description |
|---|---|
| 1–7 | Class: Festuco-Brometea (calcareous lowland grasslands)<br>Order: Brometalia erecti (dry and semi-dry grasslands)<br>Alliance: Mesobromion erecti<br>Sub Alliance: Seslerio-Mesobromion (short grassland) |
| V | Class: Violetea calaminariae (vegetation on soils rich in heavy metals)<br>Order: Violetalia calaminariae<br>Alliance: Thlaspion calaminariae (pioneer communities of the class) |
| ▲ | Class: Montio-Cardaminetea (vegetation of spring-heads)<br>Order: Montio-Cardaminetalia<br>Alliance: Cratoneurion commutati (vegetation of tufaceous springs) |
| 19–22 | Class: Molinio-Arrhenatheretea (cultivated rich pastures and marshy meadows)<br>Order: Arrhenatheretalia (species-rich meadows and pastures)<br>Alliance: Ranunculo-Anthoxanthion (sub-alpine meadows and pastures) |
| 15–18 | Class: Parvocaricetea (short-sedge marsh)<br>Order: Caricetalia nigrae (mesotrophic sedge marsh)<br>Alliance: Caricion curto-nigrae |
| 8–14 | Order: Tofieldietalia (calcareous sedge marsh)<br>Alliance: Caricion davallianae |
| 23 | Class: Oxycocco-Sphagnetea (bogs and wet heaths)<br>Order: Ericetalia tetralicis (wet heaths)<br>Alliance: Ericion tetralicis |
| 24, 28 | Order: Sphagnetalia magellanici (ombrogenous bogs)<br>Alliance: Erico-Sphagnion |
| 25, 27, 29 | Class: Nardo-Callunetea (grass heath)<br>Order: Nardetalia (acid grassland)<br>Alliance: Violion caninae |
| 26<br>31, 32, 33 | Order: Calluno-Ulicetalia (heath)<br>Alliance: Empetrion boreale |
| 1–X | Vegetation of uncertain phytosociological-affinities and fragmentary units.<br>(For details see booklet) |
| 25/9 | Complex of hummock-hollow vegetation: 25 forming hummocks, 9 forming hollows. |
| V 21 | Complex of two Alliances along line of old mineral vein: V along sides of channel, 21 on base. |
| 5, 33 | Complex of two Alliances: mosaic of units as indicated. |
| | Areas without vegetation—natural or man-made |

Aerial photography dated Oct. 1969 by Meridian Airmaps Ltd., Lancing, Sussex.

Field survey for control of photogrammetric mapping by Department of Surveying, University of Newcastle upon Tyne.

Vegetation survey prepared from ground observations and air photograph interpretation by A. V. Jones, B.Sc., University of Durham.

Photogrammetric mapping and fair drawing by M. S. Evans, Department of Surveying, University of Newcastle upon Tyne.

Additional cartographic work and printing by A. W. Gatrell & Co. Ltd., London.

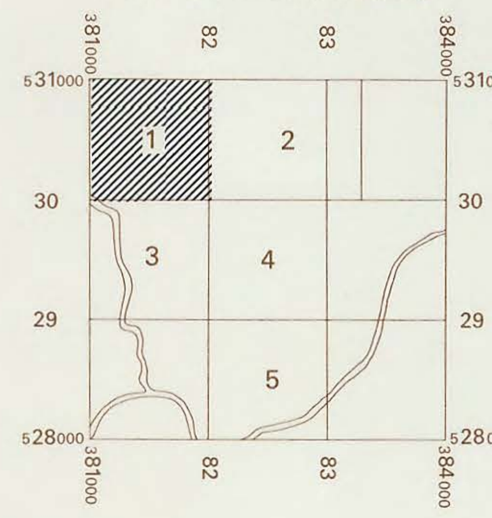
### LEGEND

| | |
|---|---|
| river, stream, sike | |
| surface water | W |
| fence, wall | |
| road, track *(fenced and unfenced)* | |
| building | |
| contours (metres) | 500 |
| spot level (metres) | . 525·6 |

This sheet is one of a series of five maps at 1:2500 scale which cover Widdybank Fell, part of the Upper Teesdale Nature Reserve.

The maps are the result of a research project financed by the Teesdale Trust and carried out in the Universities of Durham and Newcastle upon Tyne under the supervision of M. E. Bradshaw, Ph.D. and I. Newton, M.Sc.

### INDEX TO ADJOINING SHEETS




Additional maps, together with a descriptive booklet by M. E. Bradshaw, Ph.D. and A. V. Jones, B.Sc., outlining the classificatory system used, are available from:–The Secretary,
Department of Extra-Mural Studies,
University of Durham,
32 Old Elvet,
Durham.

# WIDDYBANK FELL

1:10000

Vegetation


## VEGETATION CLASSIFICATION

**1** Class: Asplenietea rupestris (wall and scree communities)
Order: Androsacetalia vandellii (communities of Siliceous rocks)

**2** Class: Festuco-Brometea (calcareous lowland grasslands)
Order: Brometalia erecti (dry and semi-dry grasslands)
Alliance: Mesobromion erecti
Sub Alliance: Seslerio-Mesobromion (short grassland)

Class: Violetea calaminariae (vegetation on soils rich in heavy metals)
Order: Violetalia calaminariae
Alliance: Thlaspion calaminariae (pioneer communities of the class)

**3** Class: Molinio-Arrhenatheretea (cultivated rich pastures and marshy meadows)
Order Arrhenatheretalia (species-rich meadows and pastures)
Alliance: Ranunculo-Anthoxanthion (sub-alpine meadows and pastures)

**4** Class: Parvocaricetea (short-sedge marsh)
Order: Caricetalia nigrae (mesotrophic sedge marsh)
Alliance: Caricion curto-nigrae

**5** Order: Tofieldietalia (calcareous sedge marsh)
Alliance: Caricion davallianae

**6** Class: Oxycocco-Sphagnetea (bogs and wet heaths)
Order: Ericetalia tetralicis (wet heaths)
Alliance: Ericion tetralicis

**7** Order: Sphagnetalia magellanici (ombrogenous bogs)
Alliance: Erico-Sphagnion

**8** Class: Nardo-Callunetea (grass heath)
Order: Nardetalia (acid grassland)
Alliance: Violion caninae

**9** Order: Calluno-Ulicetalia (heath)
Alliance: Empetrion boreale

Areas with vegetation of two Alliances

Alliance only occupying 80–95% of the area

Areas without vegetation—natural or man-made

**A–W** Complexes of a number of Alliances and unclassified vegetation

| | | | | | |
|---|---|---|---|---|---|
| A | 3, 9 | H | 4, 5, 6, 9 | Q | 3, 4, 5 |
| B | 2, 3, 5, 7, 9 | J | 2, 3, 5, 7, 8, 9 | R | 4, 5, 8 |
| C | 2, 3, 4, 5, 8, 9 | K | 2, 3, 4, 5, 9 | S | 2, 3, 4, 8, 9 |
| D | 2, 3, 4, 5, 7, 8, 9 | L | 3, 4, 5, 9 | U | 4, 8 |
| E | 6, 7, 9 | N | 2, 3, 8 | W | 2, 3 |
| F | 4, 5, 8, 9 | P | 2, 3, 9 | | |

G Soligenous mire with high covers of *Juncus effusus*

T Scattered tufts of vegetation amongst baked marl fragments

1000 500 0 feet 1000 2000 3000

500 400 300 200 100 0 metres 500 1000

SCALE 1:10,000

Heights in metres above Ordnance Datum.

Contour interval 10 metres

## LEGEND

| | | | |
|---|---|---|---|
| river, stream, sike | | contours (metres) | 500 |
| road, track | | spot level (metres) | . 513 0 |
| footpath | | | |
| fence, wall | | | |
| building | | | |


Aerial photography dated June 1969 by Meridian Airmaps Ltd., Lancing, Sussex.

Field survey for control of photogrammetric mapping by Department of Surveying, University of Newcastle upon Tyne.

Vegetation survey prepared from ground observations and air photograph interpretation by A. V. Jones, B.Sc., University of Durham.

Photogrammetric mapping and fair drawing by M. S. Evans, Department of Surveying, University of Newcastle upon Tyne.

Additional cartographic work and printing by A. W. Gatrell & Co. Ltd., London.

This map is the result of a research project financed by the Teesdale Trust and carried out in the Universities of Durham and Newcastle upon Tyne under the supervision of M. E. Bradshaw, Ph.D. and I. Newton, M.Sc.


Five large-scale maps (1:2500) of those areas on Widdybank Fell with vegetation on calcareous substrata and a descriptive booklet by M. E. Bradshaw, Ph.D and A. V. Jones, B.Sc., outlining the classificatory system used, are available from:
The Secretary,
Department of Extra-Mural Studies,
University of Durham,
32, Old Elvet,
Durham.